DIFFERENTIAL HABITAT SELECTION OF BLACK BEARS, GRAY WOLVES, AND BOREAL CARIBOU IN THE BOREAL SHIELD OF SASKATCHEWAN

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ABSTRACT

Boreal woodland caribou (*Rangifer tarandus caribou*) are listed as Threatened on Schedule 1 of the Canada *Species at Risk Act*, and critical habitat for this species is currently being defined across the country. Declines in populations have been driven largely by anthropogenic disturbance, and in this context much research has been directed at caribou habitat selection and that of their predators, including wolves (*Canis lupus*) and black bears (*Ursus americanus*). However, in the Boreal Shield of Saskatchewan caribou occur in relatively pristine habitat with low levels of anthropogenic disturbance, a naturally high fire-return interval, and few invasive species. The objectives of my study were to: (i) provide novel information on black bear and wolf ecology in the Boreal Shield of Saskatchewan; (ii) provide a baseline of data from a northern caribou range to which bear-wolf-caribou habitat selection patterns obtained from areas of greater anthropogenic disturbance can be compared; and (iii) examine how the species overlap in habitat selection patterns during the critical calving and post-calving seasons and relate that to potential for predation by black bears relative to wolves. My study was the first of its kind in northern Saskatchewan. Using satellite radio-tracked black bears, wolves, and caribou, I determined that bear habitat selection was strongly phenological, with animals generally selecting for mixed coniferous-deciduous stands in the first half of the active season but transitioning towards selecting younger (berry-producing) coniferous stands, especially jack pine forests, later in the summer and into fall. Bears also showed selection for linear features like roads and trails, and lower elevations (which included drainages). Wolves consistently avoided mature black spruce, a potential caribou refuge, but strongly selected open muskeg habitats, potential habitats for multiple prey species including caribou and moose. Wolves also selected lower elevations but unlike bears they showed an avoidance of linear features. During times of peak calf vulnerability, caribou appeared to maintain spatial separation from both predator species but were able to separate more strongly from bears than wolves. In my study area, I conclude that wolves rather than bears are still likely the most important predator influencing caribou populations considering relative overlap in habitat selection patterns. My results will help inform management decisions for caribou of the Saskatchewan Boreal Shield, with relevance to other northern boreal caribou populations that range over areas where disturbance is largely natural and not strongly influenced by human activity.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Habitat selection

The study of how animals non-randomly use habitat is an established, central theme of wildlife ecology. The process, termed habitat selection, can be defined as the scale-dependent, behavioural process by which individuals use a non-random set of available habitat features or resources in order to maximize their fitness under existing ecological and physiological conditions (Johnson 1980, Rosenzweig 1981, Morris 2003b). As a behaviour, habitat selection is expected to reflect traits under natural selection (Morris 2003b). While relative use of habitat features or resources by organisms is rooted in innate selection processes, habitat selection can also be influenced by learning behaviour (Nielsen et al. 2013, Johnson and Crane 2018). Regardless of the potential genetic or learned basis for habitat selection, selection studies can reveal drivers of habitat selection. For example, habitat selection by individuals is hypothesized to be under the influence of predation (Rettie and Messier 1998), competition (Rosenzweig 1981), intra- and inter-specific density dependence (Fretwell and Lucas 1969, van Beest et al. 2014), anthropogenic impacts (Takahata et al. 2014), natural disturbance (Brawn et al. 2001); and food availability (Costello and Sage Jr 1994). As such, the process dictates the distribution of animals through space and time with implications for population dynamics, interspecific interactions, and coevolution (Rosenzweig 1991, Morris 2003b).

Habitat selection is often modelled using logistic regression to compare habitat units that are known to be used by an individual to those habitat units are potentially available or known to be unused by an individual (Boyce et al. 2002, Manly et al. 2002). These models often take the form of a resource selection function (RSF), which are mathematical functions that when solved are proportional to the probability of selection of a habitat or resource unit (Lele et al. 2013). When habitat is used disproportionate to availability, a habitat unit is considered to be selected (Johnson 1980). Such selection could hint at combinations of environmental conditions that help species satisfy vital life history functions (Johnson 1980, Boyce and McDonald 1999).

Researchers now recognize that habitat selection is an inherently scale-dependent process in both space and time. Patterns of distribution and resource use can differ at a variety of

spatiotemporal scales. Habitat selection is hierarchical beginning with the geographic range of a species, through to selection of food items (Johnson 1980). Rettie and Messier (2000) proposed that habitat selection should reflect a hierarchy of factors that could potentially limit fitness. The hypothesis states that the most limiting factor should drive selection at broader scales and be less influential at finer scales until the next most limiting factor becomes most important. These limiting factors can vary with environmental characteristics and habitat heterogeneity, but, at broader scales, animals should select for habitat to avoid predation (Creel et al. 2005, McLoughlin et al. 2005, Dinkins et al. 2014), competition (Wereszczuk and Zalewski 2015, Duquette et al. 2017), and human mortality risk (Basille et al. 2013, Stillfried et al. 2015) while animals should select for high quality forage at finer scales (Fortin et al. 2005, Boyce 2006). However, selection can operate at different scales for different species, and can involve more than one explanatory variable that may also operate at different scales themselves (Wiens 1989, Mayor et al. 2009, McGarigal et al. 2016).

Multi-scale habitat selection studies are better able to predict limiting factors for populations and better inform management and conservation decisions (Wiens 1989, DeCesare et al. 2012). Studies executed across single scales cannot be extrapolated as often there exists a decoupling of trends found at one scale versus another, smaller or larger scale (Wiens 1989). The importance of multi-scale analyses has been well-recognized in ecology, hundreds of studies have been conducted observing behaviours at two or more scales (Heisler et al. 2017) often referenced within a hierarchical framework as proposed by Johnson (1980). Referring to such hierarchy is generally intended to facilitate comparison between studies but often is misinterpreted and wrongly assigned by authors whose studies don't fit perfectly into the hierarchy or whose studies are of a different approach altogether (Wheatley and Johnson 2009, Heisler et al. 2017). Furthermore, Mayor et al. (2009) concluded that choosing scales based on arbitrary, pre-defined levels such as those suggested in Johnson (1980) can ignore selection along a full gradient of scales at which explanatory variables may be operating.

Ecologists often ignore the temporal aspect of scale, instead focusing heavily on spatial scale (Mayor et al. 2009, Heisler et al. 2017). Habitat selection of organisms can vary daily (Martin et al. 2010), seasonally (Bennitt et al. 2014), annually (Schooley 1994), or between various life stages (Stamps 2001). Conditions that drive habitat selection, such as predation, forage availability, or human activity can also vary across time and space (Mayor et al. 2009).

Spatial and temporal scales are linked, with increased spatial scale, the time scale of important processes increase as such processes occur at slower rates in addition to the increased importance of time lags and indirect effects (Wiens 1989).

1.1.1 Habitat selection of predators and prey

Habitat selection is not purely driven by habitat itself, as a variety of organismal interactions and environmental impacts shape habitat selection. Predator-prey dynamics are one important driver of habitat selection (Sih 2005): prey do not forage in patches independent of predation risk (Morris 2003b), nor do predators travel landscapes independent of prey-searching behaviour (Sims et al. 2006).

It has long been thought that predator avoidance is a primary factor influencing habitat selection patterns at broader scales for prey (Rettie and Messier 2000, Creel et al. 2005), which often involves reducing spatial and temporal overlap with predators (Sih 2005). As organisms select patches of high forage abundance and quality (Pyke et al. 1977), these patches may become high-quality food patches for predators (Petranka 1989). Hence, for prey, there is often a tradeoff between foraging in optimal habitat and predator avoidance (Sih 1980). One solution for prey to avoid predators is to forage in what otherwise would be classed as suboptimal forage habitat (Heithaus and Dill 2002). Also, temporal separation may occur when prey forage during periods of predator inactivity (Tambling et al. 2015). Differential resource selection and partitioning is a key facet of behavioural and evolutionary ecology as it is one of the principal relationships that permit species to coexist (Rosenzweig 1981;1991, Wootton 1992, Morris 2003b).

Compromising forage quality and quantity to avoid predators may offer fitness benefits (Petranka 1989); however, avoiding one predator can also increase predation risk by another. This idea has been termed predator facilitation (Charnov et al. 1976). Hence, in multi-predator environments, prey have to manage responses to different predators with potentially different hunting strategies (Kotler et al. 1992). Conversely, predators select habitat that maximizes the likelihood of encountering prey (Milakovic et al. 2011). While it may seem simple enough to assume that predators select for habitats where prey density is highest (Carbone and Gittleman 2002), this is not always the case as both predators and prey can respond to one another simultaneously: predation risk and subsequent prey and predator presence across a landscape can therefore be continuously changing (Lima 2002). An alternate strategy to mitigate mobile prey,

is to track areas where prey forage habitat is abundant rather than prey itself (Flaxman and Lou 2009). As a result, this predator-prey space race can lead to prey under-matching their own resources to decrease predation risk while predators may match the distribution of prey habitat but not prey distribution itself (Sih 2005). Empirical studies with predators and prey moving freely across the landscape have found varying results (Benoit-Bird and Au 2003, Hammond et al. 2007, Luttbeg et al. 2008, Laundré 2010, Petrunenko et al. 2016).

Habitat selection by predators does not exclusively reflect selection for prey. Patterns of habitat selection can also reflect life stages such as mating (Singh et al. 2016), denning (Szor et al. 2008), nesting (Titus and Mosher 1981), or dispersal (Palomares et al. 2000). All these factors are summarized when examining habitat selection across broader spatial or temporal scales. Intermediate predators also face predation, therefore they can show habitat selection responses to the threat of predation as well (Mukherjee et al. 2009). Human activity and mortality risk towards top predators can elicit a response similar to predator avoidance. For example, brown bears (*Ursus arctos*; Northrup et al. 2012), cougar (*Felis concolor*; Wilmers et al. 2013*),* spotted hyena (*Crocuta crocuta;* Boydston et al. 2003), and grey wolves (*Canis lupus;* Whittington et al. 2005) have all been found to avoid linear features with high levels of human activity. African lions (*Panthera leo*) increase their use of thicker brush cover when in closer proximity to human activity (Schuette et al. 2013). Tigers (*Panthera tigris*) in human occupied areas shift their activities to dark hours when human activity is low (Carter et al. 2012). Both predator and prey habitat selection is a dynamic process to gain forage and avoid mortality threats, often these processes are compounded by disturbance.

1.1.2 Habitat selection and human disturbance

Human disturbance can influence habitat selection patterns of both prey and predator species. In general, organisms aim to avoid disturbance but it varies based on disturbance type and tolerance of human activity (Muhly et al. 2011, Rogala et al. 2011, González-Bernal et al. 2016). Certain disturbance types can provide preferable forage for species. For example, wolverine (*Gulo gulo*) in Alberta selected for logging cutblock edges that provide foraging opportunities (Scrafford et al. 2017). Early-seral forest stands created by logging cutblocks are also known to provide browse for ungulates such as moose (*Alces alces*; Rempel et al. 1997) and deer (*Odocoileus* sp.; Dawe et al. 2014). Many species show favored use of human-created linear features on the landscape (Barding and Nelson 2008, Andersen et al. 2017). Linear features facilitate movement

and food searching across the landscape (Tigas et al. 2002, Dickson et al. 2005, Dickie et al. 2017). Most prominent is the example of wolf use of linear features across Canada with implications for their prey across the landscape (discussed further in section 1.4 *Gray wolves*).

Habitat alteration can modify habitat selection such that it facilitates apparent competition (Robinson et al. 2002, Bryant and Page 2005, Wittmer et al. 2007), termed habitat-mediated apparent competition (Hervieux et al. 2014). Apparent competition occurs when one prey species indirectly causes the decline in another species by way of a common predator (Holt 1977). Apparent competition can be mediated by landscape disturbance, human-caused or natural, which acts to increase the overall abundance or biomass of alternate prey by providing preferable habitat or forage (Robinson et al. 2002, Wittmer et al. 2007, DeCesare et al. 2010), which in turn attract predators into habitats (Bergerud and Elliot 1986, Seip 1992). The increase in predator numbers leads to an increase in predation on the original prey species (Wittmer et al. 2005, Wittmer et al. 2007). Combined with the efficiency of using anthropogenic linear features like roads, trails, and geophysical survey lines for searching and hunting by large predators, habitat-mediated apparent competition can have significant effects on already struggling populations (DeMars and Boutin 2018).

Regardless of the potential for some species to use human-modified habitats, a global review by Gaynor et al. (2018) found that, across all habitat and disturbance types, species increased nocturnal activity in response to human disturbance. Temporal shifts in activity can facilitate some usage of preferable or beneficial disturbance features while maintaining separation from human activity and associated risks (Hebblewhite and Merrill 2008, Eldegard et al. 2012). Avoidance of human activity has been observed in large predators (Muhly et al. 2011, Wilmers et al. 2013), sometimes to greater effect than avoidance of human activity by their prey. As a result, human activity can act as a refuge for prey species (Muhly et al. 2011, Brzeziński et al. 2018).

1.1.3 Habitat selection in conservation

With humans creating unprecedented change across the globe, species have been dramatically affected by alteration and destruction of habitat (Morris 2003a). In addition to human-driven landscape change, climate change plays a role in shaping species distributions and habitat selection patterns. As climate warms and ecosystems shift, habitat selection patterns by species can be disrupted by the loss or shift of preferred habitat (Staudinger et al. 2013). Understanding

current and past habitat selection of a species can help researchers interpret the impacts of climate change on a species and potentially predict future shifts in habitat selection or population declines (Morris et al. 2012, Wilson et al. 2016, Brambilla et al. 2018). In addition, species may exhibit finer-scale behavioural shifts that allow them to remain in a similar distribution with adjusted selection patterns to make it more suitable(van Beest et al. 2012, Pigeon et al. 2016, Beever et al. 2017, Hobbs et al. 2018). Species are responding to climate change in complex, variable, and unexpected ways often resulting in novel ecological communities and interactions (Staudinger et al. 2013) and it is important to keep these effects in mind when interpreting habitat selection studies. Because of these landscape and climate change impacts, conservation and management have become the driver and focus of many studies.

Developing management strategies for conservation of a species involves a necessary understanding of the factors controlling a species' population dynamics and distributions. Habitat selection, modelled by resource selection functions, allows managers and researchers to understand distribution patterns at multiple scales across a species current range. Combining habitat selection studies with demographic data can identify critical habitat necessary for a population or species survival (McLoughlin et al. 2006, Uboni et al. 2017). The same habitat analysis techniques can be used to consider potential future habitats for species expansions, re-introductions, or shifts following climate change (Hebblewhite et al. 2011, Bleyhl et al. 2015, Pietrek and González-Roglich 2015, Paton and Matthiopoulos 2016), but often extrapolation of habitat selection studies are difficult. Landscape-specific differences in habitat may render selection metrics incomparable between locations (Graf et al. 2006). Additionally, differences in demography or behaviour across spatially distinct populations can result in differences in habitat selection patterns between populations (Beyer et al. 2010). These differences can limit the predictive power of habitat selection models. Multi-scale habitat selection studies have greater predictive power of limiting factors for populations (Wiens 1989, DeCesare et al. 2012). Studies executed across single scales cannot be extrapolated as often there exists a decoupling of trends between scales (Wiens 1989). Studies over small spatial and temporal scales only represent a subset of the variation influencing population persistence (Schneider 2002, Heisler et al. 2017).

As human expansion and subsequent habitat destruction continues, the potential for human-wildlife conflict also grows. Human-wildlife conflict is the interaction between humans and wildlife that result in negative impacts on human interests including social, economic, or

cultural, and on the conservation of wildlife populations (Swan et al. 2017). Understanding how animals select for habitat in light of human disturbance and activity is key to mitigating human-wildlife conflict. The literature on how animals respond across various landscapes of human presence is substantial and from it, researchers can model risk of conflict across various human-disturbed landscapes (Sitati et al. 2003, Treves et al. 2004, Burdett et al. 2010, Mateo-Tomás et al. 2012). Humans are the driver of these conservation measures and conflict issues but information can still be extracted from lower-use areas. If habitat selection, conflict, and conservation can be assessed in highly disturbed areas, it is then useful to contrast it with regions or species that do not face the same circumstances.

1.2 Boreal woodland caribou

Woodland caribou (*Rangifer tarandus caribou*) are a subspecies of caribou that exist across a variety of habitats in the forested mountain and boreal regions of Canada. Boreal caribou, hereafter 'caribou', are a geographically distinct, forest-dwelling ecotype of woodland caribou that tends to be sedentary rather than migratory. Woodland caribou are a Threatened species listed on Schedule 1 of the Canada *Species at Risk Act* (Environment Canada 2012). Reasons for the risk status vary throughout the species' distribution, but human disturbance is considered of high significance in contributing to population declines (Environment Canada 2012).

Many boreal caribou ranges intersect areas of high timber, oil, natural gas, mineral, and peat extraction or harvesting. These activities lead to significant alteration, fragmentation, or complete destruction of large tracts of habitat that are important to caribou. However, populations of caribou require large, continuous tracts of mature conifer forests and muskegs or peatlands for foraging, mating, and calving (Environment Canada 2012); to provide adequate dispersal habitat following natural disturbances (Environment Canada 2012); and to facilitate predator avoidance through spatial segregation from predators and alternate prey (Bergerud and Page 1987). In addition to loss of habitat, human activities and subsequent habitat destruction have indirect effects on caribou. These indirect effects take the form of habitat-mediated apparent competition, a type of apparent competition (Holt 1977). In the case of caribou, it is hypothesized that human disturbance leading to conversion of mature forests to early seral stands causes an increase in densities of alternate prey species such as moose (Rempel et al. 1997) or deer (Latham et al. 2011), which results in a numerical response from predators (usually wolves;

Messier 1994), and subsequent increase in predation on caribou (Seip 1992, Wittmer et al. 2005, Wittmer et al. 2007).

In 2012, the Canadian government released a *Recovery Strategy* for the boreal caribou to guide implementation of recovery actions (Environment Canada 2012). Environment Canada (2011) defined 51 ranges or management units for boreal caribou. Researchers conducted a meta-analysis across all caribou ranges to define a relationship between calf recruitment and total disturbance (i.e., natural and anthropogenic). The resulting relationship was used to assess the probability that habitat within each range could support a self-sustaining populations of caribou (Environment Canada 2011). The assessment indicated that only 14 of the 51 ranges were "self-sustaining". Of the remaining 37 ranges, 26 were "not self-sustaining", 10 ranges were "likely not self-sustaining", and one, the Saskatchewan Boreal Shield (SK1) range, was considered "unknown" (Environment Canada 2011). The "unknown" designation of the SK1 range was due to the levels of natural fire and anthropogenic disturbance that fell outside the range of values used to define the relationship between calf recruitment and disturbance. The SK1 range could not be assessed using the existing model. In addition, at the time of the recovery strategy publishing, there were no trend data available for SK1 and they were unable to identify critical habitat in the range (Environment Canada 2012).

As evidenced by Environment Canada's (2012) recovery strategy, most research on caribou in Canada has been directed at highly modified landscapes where forestry and oil and gas industry contribute most to disturbance in the area; however, caribou in the Boreal Shield of Saskatchewan are faced with low anthropogenic disturbance and high levels of fire disturbance. Less than 3% of the area occurs within 500 meters of industrial features (e.g. roads, transmission lines, settlements, mines), but over 55% of the area has been mapped as burned in the last 40 years (Environment Canada 2012). The Saskatchewan Boreal Shield stands out as a relatively 'intact' ecosystem: all of the expected predators (e.g., wolves [*Canis lupus*], black bears [*Ursus americanus*]) and alternate prey (moose [*Alces alces*], beaver [*Castor Canadensis*]) occur, but without the invasive species (e.g., coyotes [*Canis latrans*], white-tailed deer [*Odocoileus virginianus*]) known from more southern ranges (McLoughlin et al. 2016). In response to the federal recovery strategy, the University of Saskatchewan partnered with the Province of Saskatchewan (Ministry of Environment), Environment and Climate Change Canada, and several additional governmental, industrial and academic groups to launch the Saskatchewan Boreal

Shield Woodland Caribou Project. The project combined habitat selection studies, demographic models, and vegetation surveys to assess critical habitat for caribou in the SK1 range.

In 2014, 94 caribou were collared in the SK1 range and tracked until 2018. Collaring and subsequent relocation efforts provided the opportunities to estimate pregnancy rates, population structure, survival, recruitment, and population growth (for detailed methods see McLoughlin et al. 2019). McLoughlin et al. (2019) found that caribou of the Saskatchewan Boreal Shield encompass a relatively large population that is fluctuating but stable in trend. Caribou in the study area are characterized by high annual adult survival and moderate calf recruitment. Density of caribou in the study area were estimated to be high (36.9 caribou per 1000 km^2), up to 3 times as high as the average for other ranges (McLoughlin et al. 2019). In addition to information on population demography, the collared caribou were used to assess habitat selection in the Boreal Shield of Saskatchewan. Superbie et al. (2019) found that mature jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) forests, treed bogs, and open muskegs were important habitats for caribou across seasons and scales, with stands of mature jack pine being the key habitat selected in winter and black spruce swamps at calving. They found effects of linear features were highly scale-dependent. At the population scale, females were always more likely to occur at lower elevation and closer to linear features; however, within home ranges, caribou were more likely to be found farther from linear features and at generally higher elevation during the snow-free seasons, and closer to linear features with no effects of elevation in winter. Due to lack of data on predators of caribou in the SK1 range, proxies were used to analyze predation risk and forage availability. Assumptions were made about how the proxies influenced behavioural strategies adopted by caribou to manage risk-forage tradeoffs.

1.3 Black bears

Black bears (*Ursus americanus*) are common throughout forested areas of North America. The species continues to inhabit most of their historical range in Canada and as such, are deemed not at risk by COSEWIC (1999a). Bears are a generalist, omnivorous species (Garshelis 2009) which allows them to exploit a variety of habitats efficiently. Bears tend to eat grasses, forbs, deciduous plants, and insects including ants during the spring and summer and switch to higher calorie soft- and hard-mast plants in the fall, adjusting as they become temporally available (Mosnier et al. 2008, Romain et al. 2013, Lesmerises et al. 2015). Bears are opportunistic predators, known to be effective predators of ungulate calves, specifically in the first four to six weeks of life when

they are most vulnerable (Bergerud 1971, Ballard et al. 1981, Pinard et al. 2012, Mahoney et al. 2016). In other caribou ranges, black bears have potential to impact caribou populations through calf predation (Pinard et al. 2012, Leblond et al. 2016).

It is exactly that opportunistic adaptability of black bears that can lead to conflict with humans. Bears go through periods of hyperphagia, i.e. intensive foraging, prior to denning through the winter (Lewis et al. 2015). In year of forage crop failure, or low productivity environments, bears struggle to consume sufficient calories resulting in pursuit of alternative food sources (Baruch-Mordo et al. 2014). Use of anthropogenic food sources can lead to behavioural changes, changes to bear ecology, and human-black bear conflicts (Beckmann and Berger 2003a, Baruch-Mordo et al. 2008). Intentional use of anthropogenic food has been used as a diversionary feeding method, using food to lure bears away from areas where they are unwanted or could cause human-black bear conflicts (Garshelis et al. 2017). Conflicting results exist on the effectiveness of diversionary feeding with some successes and others showing an increase in human-black bear conflicts associated with diversionary feeding (Garshelis et al. 2017). Anthropogenic food is also used as bait for tourism and hunting purposes (Hristienko and McDonald 2007, Massé et al. 2014). Typically baits consist of high-calorie foods including meat and fish but not excluding sugars such as candy or baked goods (Kirby et al. 2017). Kirby et al. (2017) found baits to occur at a density of $\geq$0.25 bait stations per km^2 on public lands contributing over 40% to diets of 180 black bears.

Anthropogenic food sources can lead to bears exhibiting behavioural changes including having smaller home ranges and higher local density (Beckmann and Berger 2003b, Massé et al. 2014). Fersterer et al. (2001) found that bait sites did not reduce home range sizes but did lead to a local density increase. The studies by Beckmann and Berger (2003b), Massé et al. (2014), and Fersterer et al. (2001) involved anthropogenic food sources for non-hunting related purposes. Czetwertynski et al. (2007) found that home range sizes were greatly inflated in a hunted population of black bears. Hunting can influence bear habitat selection patterns. Brown bears in Scandinavia chose resting sites with greater cover during the day and farther from human settlements during the hunting season (Ordiz et al. 2011). In addition, brown bears in Scandinavia adjusted their activity patterns with increased movements during dark hours during the hunting season (Ordiz et al. 2012). Black bears in Michigan were found to trade-off avoidance of paved roads (vehicular collision risk) with non-paved roads (hunter risk). Bears

avoided non-paved roads more strongly than paved roads during hunting season and reduced their activities and road crossings to dark hours (Stillfried et al. 2015). Bear response to human risk is evident but the majority of studies on the topic center around areas where human development and potential conflict are the focus (Johnson et al. 2015, Lewis et al. 2015, Hertel et al. 2016, Duquette et al. 2017), which is to be expected as mortality risk is positively associated with human presence and access (Steyaert et al. 2016). It is unclear how bears respond to human risk, such as hunting, in areas away from major human development.

We know very little about bears in Saskatchewan. Population size in the province is assumed to be stable or increasing although this assumption in not quantitatively supported (Saskatchewan Ministry of Environment 2018). Previous attempts to measure population size lack consistent data and methods to provide accurate estimates. The most recent estimate of provincial black bear population was 10,000 – 25,000 bears (Williamson 2002). In our study area in the Boreal Shield, bear annual home range size (95% MCP) was 317 km^2 for adult males and 80 km^2 for females of all age classes (McLoughlin et al. 2019). This home range size is much larger than has been observed in similar black bear ranges (Garshelis and Pelton 1981, Mosnier et al. 2008, Sadeghpour and Ginnett 2011, Massé et al. 2014). Given the large home ranges, it is likely that bear density in the region is among the lowest known for the species in the boreal forest (McLoughlin et al. 2019).

Even with low densities, there are enough bears to support a small hunting economy. Black bears in Saskatchewan are hunted during spring and fall seasons (April-June and August-October, respectively). Each hunter is allowed one bear of either sex with the exception of females with young-of-the-year cubs (Saskatchewan Ministry of Environment 2017).

1.4 Gray wolves

Historically, gray wolves (*Canis lupus*) had one of the most extensive ranges of any mammal (Nowak 1983). In North America, gray wolves occupied all habitats north of 20º N latitude until late nineteenth century when wolf numbers declined due to human expansion and persecution of wolves in retaliation of human-wolf conflict (Paquet and Carbyn 2003). Since then, wolf populations across Canada have rebounded, and are deemed not at risk (COSEWIC 1999b).

In Canada, gray wolf populations are generally stable but vary in legal status from province to province (Mech and Boitani 2010). In Canada, wolves retained much of their range as it retracted northward invalidating the need for reintroductions as was done famously in the

United States (Musiani and Paquet 2004). Wolf control still exists in some jurisdictions mainly for the purposes of managing human-wolf conflict (livestock predation) and ungulate populations (Musiani and Paquet 2004). In both cases, culling is met with both strong support and opposition. A recent review of peer-reviewed studies of carnivore control for livestock predation indicated uncertainties regarding the effectiveness of lethal methods (Treves et al. 2016). Most of the tests of lethal methods found no effect and non-lethal methods were more effective in preventing predation (Treves et al. 2016). Wolf control programs have demonstrated to stabilize or increase ungulate numbers (Boertje et al. 1996), but it is unclear how the relative contributions of overhunting and human development act in relation to the decline of ungulates (Paquet and Carbyn 2003). Nonetheless, wolf control has been considered as a possible means of recovery for threatened woodland caribou populations in Canada (Hervieux et al. 2014).

Wolves are a generalist, carnivorous species and their diet varies based on geographic availability of prey (Peterson and Ciucci 2010). Wolves are known to prey on hoofed mammals, small mammals such as hares or beaver, and anthropogenic food and garbage (Peterson and Ciucci 2010). As a carnivore, wolf habitat selection is driven by prey and prey-suitable habitat (Courbin et al. 2014, Kittle et al. 2017). Human activity also shapes wolf habitat selection; previous studies show a highly variable response to human landscape features. Wolves may exhibit general avoidance of human-related habitat features and human activity (Lesmerises et al. 2012, Llaneza et al. 2012), or wolves may select human-created linear features thought to increase travel rates and search efficiency (McKenzie et al. 2012, Dickie et al. 2017). Wolves have also been found to alter selection for linear features as a function of linear feature density, called a habitat functional response (Mysterud and Ims 1998). Such functional responses commonly occur when there exists a trade-off, such as the one wolves make between human-related mortality risk and food (Mysterud and Ims 1998). Studies have found that wolves select for disturbance features in areas with higher disturbance feature density (Hebblewhite and Merrill 2008, Newton et al. 2017) but the strength and direction of responses can vary between seasons, linear feature types, or study populations (Houle et al. 2010, DeMars and Boutin 2018). However, many of these studies are conducted in areas where human disturbance is high and spatial scale is limited. Muhly et al. (2019) conducted a review summarizing wolf habitat selection throughout Canada across a variety of linear feature densities. They found a positive functional response of wolves to both linear features and forest harvest cutblocks. While wolves

may generally select for linear features in high feature-density areas, humans still pose a risk to wolves and as such may be avoided. For example, Hebblewhite and Merrill (2008) showed that wolves displayed a functional response for proximity to humans as human activity increased; however, wolves avoided human activity temporally during daylight.

Similar to black bears, we know very little about wolf populations in Saskatchewan. There are no formal population surveys of wolves in Saskatchewan (Saskatchewan Ministry of Environment 2017). Provincial populations were estimated in 2006 using two methods, a linear regression model and a habitat model, resulting in an estimated 2719–3773 wolves (see Saskatchewan Ministry of Environment 2017). In my study area in the Boreal Shield, wolf home ranges were notably large averaging 3316 ± 751 km^2 (95% AKDE) and subsequent densities were low (3.1 wolves/1000 km^2; Neufeld et al. 2019). In addition, average pack sizes are small (4.0 wolves/pack), not unusual for a low-density population (Neufeld et al. 2019). Wolves in Saskatchewan are furbearers and can be trapped during the winter season (October-March). Since 2014, the Saskatchewan government has implemented a wolf hunting season in the winter (October-March) to manage wolf-human conflict (livestock losses) in certain areas (Saskatchewan Ministry of Environment 2017). Culling of wolves is legal for protection of livestock but currently not done to protect wild ungulates (Musiani and Paquet 2004).

1.5 Objectives and thesis structure

The objectives of my study were to: (i) provide novel information on black bear and wolf ecology in the Boreal Shield of Saskatchewan; (ii) provide a baseline of data from a northern caribou range to which bear-wolf-caribou habitat selection patterns obtained from areas of greater anthropogenic disturbance can be compared; and (iii) examine how the species overlap in habitat selection patterns during the critical calving and post-calving seasons and relate that to potential for predation by black bears relative to wolves. My thesis is laid out in manuscript-style according to the guidelines set forth by the College of Graduate Studies and Research at the University of Saskatchewan and as such, there is some repetitive information as it pertains to more than one chapter in my thesis. Chapter 1 of my thesis covers background information that shapes the ideas in my thesis. In Chapter 2, I meet the above objectives with respect to black bears. Chapter 2 is a manuscript assessing black bear habitat selection in the Boreal Shield of Saskatchewan and how it relates to woodland caribou. Chapter 3 matches the style and ideas of Chapter 2 but pertains to gray wolves. The latter is a manuscript assessing wolf habitat selection

in the Boreal Shield of Saskatchewan and how it relates to both woodland caribou and black bears. Overall, my hope is that my results will help inform management decisions regarding caribou, black bears, and wolves and uncover potentially important factors relevant to these species in Saskatchewan and Canada.

1.6 Literature cited

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CHAPTER 2: HABITAT SELECTION BY BLACK BEARS IN THE BOREAL SHIELD OF SASKATCHEWAN

2.1 Introduction

Predator-prey relationships are an important driver of population dynamics as predators influence survival (Sinclair et al. 1998, Kramer and Drake 2010), growth rates (Van Buskirk and Yurewicz 1998), distribution (Thaker et al. 2011), and behaviour (Nelson et al. 2004) including reproduction and competitive interactions of prey populations. However, the impact of a predator on a prey population cannot be generalized as such impacts are influenced by a variety of factors, such as habitat heterogeneity (Gorini et al. 2011), spatiotemporal variation in the availability of alternative prey species (Hebblewhite et al. 2003, Knopff et al. 2010), the presence of other predators (Tallian et al. 2017), and predator–prey body size relationships (MacNulty et al. 2009, Périquet et al. 2012).

Black bears (*Ursus americanus*) and grizzly bears (*Ursus arctos*) are generalist, omnivores (Garshelis 2009) and hence their foraging decisions can have a large impact on populations at multiple trophic levels (Closs et al. 1999). Bears can display a broad range of search tactics for their food sources and, as such, are considered more opportunistic predators than obligate carnivores (Zager and Beecham 2006, Bastille-Rousseau et al. 2011, Latham et al. 2011). Both grizzly and black bears are known to be effective predators of ungulate calves, specifically in the first four to six weeks of life when they are most vulnerable (Bergerud 1971, Ballard et al. 1981, Pinard et al. 2012, Mahoney et al. 2016). Several studies across North America have shown that black bears and grizzly bears are important predators of neonatal elk (*Cervus canadensis;* Smith and Anderson 1996, Singer et al. 1997, Tatman et al. 2018), moose (*Alces alces;* Stewart et al. 1985, Ballard 1992), whitetail (*Odocoileus virginianus;* Kunkel and Mech 1994), mule deer (*Odocoileus hemionus;* Monteith et al. 2014, Shallow et al. 2015), and caribou (*Rangifer tarandus;* Ballard 1994, Leblond et al 2016, Lewis et al 2017).

Woodland caribou (*Rangifer tarandus caribou*) are formally listed as Threatened under the federal Species at Risk Act (SARA; Environment Canada 2012). While caribou have coexisted with predators for thousands of years, in some parts of caribou range intensive human

activity may have altered these predator-prey relationships (James et al. 2004). Bears are capable of preying on adult caribou but the impact of black bears on adult caribou survival is expected to be marginal compared to predation by wolves (*Canis lupus*; Zager and Beecham 2006), with wolves often attributed as the main predator responsible for adult caribou mortality (McLoughlin et al. 2003). However, many caribou populations are suffering from low calf survival and subsequent low recruitment (Hervieux et al. 2013, Serrouya et al. 2017). Because of the potential for predation of calves by bears, it is important to consider bears as a mortality source when considering caribou survival.

The predator-prey relationship between caribou and bears has been relatively well-studied across Canada in highly modified landscapes, where forestry and the oil and gas industry contribute to most of the disturbance in the area (Environment Canada 2012). However, species in the Boreal Shield of Saskatchewan are faced with low anthropogenic disturbance but high levels of disturbance from lightning-struck fires (McLoughlin et al. 2019). Less than 3% of the area occurs within 500 m of industrial features (e.g. roads, transmission lines, settlements, mines), yet over 55% of the area has been mapped as being burned in the last 40 years (Environment Canada 2012). The Saskatchewan Boreal Shield stands out as a relatively natural ecosystem: all of the expected predators (e.g., wolves, black bears) and prey (caribou, moose, beaver [*Castor Canadensis*]) occur, but without the invasive species that can exacerbate predation pressure (e.g., coyotes [*Canis latrans*], white-tailed deer) known from more southern ranges (McLoughlin et al. 2016, 2019).

Black bears are deemed not at risk by COSEWIC (1999) as they occur in large numbers with one of the widest species distributions in Canada. Nevertheless, we know very little about black bears in Saskatchewan. Population size of bears in Saskatchewan is assumed to be stable or increasing, although this assumption is not quantitatively supported (Saskatchewan Ministry of Environment 2015). Previous attempts to measure population size lacked consistent data and methods to provide accurate estimates, but the most recent estimate of the provincial black bear population was 10000–25000 bears (Williamson 2002). Black bear densities are expected to be relatively low in the Boreal Shield, based on the above average home range sizes for bears in my study area (adult males: 316.5 ± 62.1 km^2; females: 79.8 ± 13.2 km^2, 95% MCP; McLoughlin et al. 2019). The low expected density is still enough to support a hunting economy, however, with

outfitting for black bears in Saskatchewan occurring during spring and fall seasons (Saskatchewan Ministry of Environment 2015).

Even less is known about the habitat selection patterns of black bears in Saskatchewan, with no published reports or papers on the topic that I could find. The purpose of my study was to assess habitat selection by black bears throughout an area used by caribou in the Boreal Shield of Saskatchewan. I assessed habitat selection by black bears across ecologically relevant seasons at two spatial scales: within the range of the study population (the "population scale") and within individual home ranges (the "home range scale"). However, the population and home-range scales might only provide patterns reflective of the generalist nature of the species (Boyce et al. 2003), which could potentially mask the impact and preferences of individual bears (Lesmerises and St-Laurent 2017). Therefore, I also analyzed individual habitat selection patterns for each bear at the home range scale. To compare habitat selection between species, I used latent selection differences (LSD; Mueller et al. 2004, Latham et al. 2011) to identify the potential for species' habitat selection overlap during the critical calving and post-calving periods for caribou.

Considering the generalist nature of black bears (Garshelis 2009) and the low productivity of the boreal forest (Pastor et al. 1996, Mosnier et al. 2008), bears would likely have to spend time searching for various resources across a variety of habitats. Therefore, I expected to observe weak patterns in habitat selection across all scales. Black bear habitat selection can also be linked to selection for certain food types as they become temporally available (Romain et al. 2013); hence, I expected selection of habitat types to change across seasons as bears changed their phenological focus on seasonally available food and caloric requirements due to sex, age, reproductive status, and hyperphagia in preparation for denning (Lesmerises et al. 2015). If bears were opportunistically preying on caribou calves, I expected to observe greater overlap of habitat selection between bears and caribou during the calving season as proximity leads to opportunity.

2.2 Methods

2.2.1 Study area

My broader study area was delimited by the borders of the Boreal Shield Ecozone of northern Saskatchewan, Canada (Figure 2.1). The study area for the population of black bears in my study was defined using a 100% minimum convex polygon (MCP) around cleaned GPS fixes (*n* =

4659), excluding dispersers (Figure 2.1). Dispersing bears were identified as sub-adult bears with large shifts in home range location or size.

Boreal Shield of Saskatchewan includes two main ecoregions: Churchill River Upland and Athabasca Plains. The Churchill River Upland is composed of Precambrian Canadian Shield bedrock with rocky outcrops and high relief (Padbury et al. 1998). The Churchill River Upland is characterized by continuous stands of jack pine and black spruce, as well as smaller areas of mixed forests comprised of black spruce interspersed with trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), balsam poplar (*Populus balsamifera*) and/or tamarack (*Larix laricina*). The Athabasca Plains Ecoregion is flatter and mainly composed of networks of sandy glacial deposits, moraines and eskers and is characterized by continuous jack pine forest (Secoy 2006). Overall, the region is relatively dry with long, cold winters and little snow and short growing seasons (Padbury et al. 1998). Over 90% of the Boreal Shield Ecozone was coniferous forest of varying stand age; mixed and deciduous forests were rare (7% area; Table 2.1). The topography of the area is rolling with numerous lakes and wetlands. Elevation averaged 440 ± 70 m, higher elevations occurred in the western half of the Ecozone. The elevation available to black bears ranged from 350 to 500 m. At the time of study commencement, total human disturbance (e.g., roads, mines, transmission lines) was extremely low in the study area (0.18% of total area; linear features at 0.14 km of lines per km^2 across the combined study area) but fire disturbance was high (46.98% of landmass being burned in the last 40 years; McLoughlin et al. 2019).

2.2.2 Capture and collaring of black bears

In May 2016, we commenced the pilot capture of black bears in the study area using culvert traps to bait and trap bears following University of Saskatchewan Animal Use Protocol 2016011 and permit 16FW051 from the Saskatchewan Ministry of Environment. In the study area, there is minimal road access to much of the study area resulting in limited capture sites. In May 2017, I collaborated with Wilderness Family Outfitters and Kane Lake Outfitters to gain access to their bait sites only accessible by ATV and foot approximately one to two kilometers from the main highway. Beginning around 06:00 – 10:00 or 14:00 – 20:00, when the bears at these sites were most active, two people were stationed at a bait site. Upon a bear's arrival to the bait site, it was darted using a low velocity Dan-Inject or PneuDart rifles with a mixture of medetomidine and Telazol®. The darts all had a VHF telemetry attachment so that the anesthetized bear could be

located in the brush using a radio receiver tuned to the frequency emitted by the dart tail. Captured bears were sexed and age estimated based on tooth wear. We administered meloxicam to all bears for pain management. We fitted bears with either Telonics TGW 4680-3 GPS/Argos radio collars or Lotek Wireless Inc. Iridium® Track M 2D collars set to fix locations every five hours and to automatically release after four years. Telonics collars were repurposed with a leather insert to stretch and rot over time (Garshelis and McLaughlin 1998, Bond et al. 2009). These collars were fitted on larger bears and male bears as they more commonly have issues with dramatic seasonal weight change and similar girth of neck and head (Koehler et al. 2001). After sample collection was complete, we administered a reversal agent, atipamezole, and the bear was placed away from the bait and potentially dangerous terrain for recovery.

2.2.3 Defining seasons for black bears

I defined seasons for black bears using dates of importance relative to bears. The hunting season for black bears in the study area occurs from April 15 to June 30 (Saskatchewan Ministry of Environment 2018). The spring/baiting season was chosen to coincide with that time period, from den emergence (late April and early May) to June 30. Following Mosnier et al. (2008) and Lesmerises et al. (2015), both of whom established three seasons based on major shifts in bear diet, with slight adjustments I designated summer as July 1 to August 31 and fall from September 1 to denning. All bears denned September 10 and October 23 in 2017, with a mean denning date of October 3.

2.2.4 Spatial scales of resource selection

For analysis of resource selection, I defined habitat availability to bears at two spatial scales of extent within each season. At the population scale, I defined availability as the 100% MCP around all of the GPS locations. For the home range scale, I defined availability for individual bears using the 95% weighted autocorrelated kernel density estimate (AKDE) available in the ctmm (continuous-time movement modelling) package (Version 0.5.3, Calabrese et al. 2016) in R statistical software (R Core Team 2018). This method explicitly accounts for spatiotemporal autocorrelation in telemetry data by calculating an appropriate smoother bandwidth given the data and an autocorrelated movement model. I used a fitted Ornstein-Uhlenbeck-F (OUF) motion model using initial model parameters obtained from visualizing the auto-correlation structure in an empirical variogram of the telemetry data (Fleming et al. 2014). I truncated individual home

ranges at the Saskatchewan Boreal Shield Ecozone boundaries. I calculated seasonal AKDEs only for those individuals that survived that season in question. I discarded AKDEs if the variogram did not asymptote meaning the bear was not monitored long enough to be able to account for spatiotemporal autocorrelation in the data. Individuals who showed movement patterns indicative of dispersal, or patterns I was unable to confidently characterize, were not considered in calculating AKDEs. For the individual bear analyses, I defined availability using the same methods as the home range scale analyses (95% AKDE).

2.2.5 Environmental covariates

I described the environment within the study area in terms of resource units defined as 30 × 30-m pixels characterized by: elevation (m), proximity (m) to linear features (e.g., major roads, trails, geophysical survey lines, fire breaks, transmission lines, etc.), and habitat type (n = 7; Table 2.1, Figure 2.2). I extracted elevation information from a raster layer (resolution = 30 × 30-m) derived from a digital elevation model in ArcGIS Desktop, v. 10.5 (ESRI, 2018). I measured the proximity to a linear feature as the Euclidean distance (m) between a point location and the edge of the closest linear feature. I used habitat classes derived from a raster layer of 27 Forest Ecosite Classes (FECs). The FECs were grouped and retained according to specific habitat features relevant to boreal woodland caribou (see Stewart 2016). The vegetation raster was updated each year with wildfire data to account for changes in forest stand age. The age threshold between the early-successional and mature forests was 40 years post-fire, chosen for expected recovery time for forage lichens for caribou (Environment Canada 2012, Stewart 2016).

2.2.6 Seasonal habitat selection by black bears

Resource selection functions (RSFs) are functions that are proportional to the probability of selection of a defined resource unit (Lele et al. 2013). Species interactions, including predator-prey, can be modelled using RSFs (Hebblewhite et al. 2005). RSF values are defined by the following log-linear equation (Manly et al. 2002):

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_n x_n) \quad (2.1)$$

where $w(x)$ is the relative probability of selection, $\beta_1, \beta_2, \ldots \beta_n$ are the selection coefficients (i.e. slopes) based on the variables, $x_1, x_2, \ldots x_n$.

For each season and scale, I generated RSFs using logistic regression to compare environmental attributes (see section *2.2.5 Environmental covariates*) of used locations (GPS

locations of black bear) to a set of randomly sampled locations (i.e. available points) within the ranges of black bears. To account for hierarchical telemetry data (i.e., relocations are nested within individual animals), I used generalized linear mixed models (GLMMs) in the lme4 package (Version 1.1-18-1, Bates et al. 2014) in R statistical software, with presence/availability as the response and animal as a random intercept (Gillies et al. 2006). In the case of the individual bear RSFs, I fit a generalized linear model (GLM) in place of the GLMM as each model only considered one individual. GLMMs were structured as logit models of the form:

$$g(x) = \ln\left[\frac{\pi(x)}{1-\pi(x)}\right] = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n + \gamma_{nj} x_{nj} + \gamma_{0j} \quad (2.2)$$

where $g(x)$ is a binomial response comparing the set of used points to available points; ln $[\pi(x)/1\text{-}\pi(x)]$ is the logit-link function relating the binomial response to the linear predictor on the right side of the equation; β_0 is the global intercept; $\beta_1, \beta_2 \ldots \beta_n$ are the beta-coefficients for the covariates $x_1, x_2 \ldots x_n$; $\gamma_{nj} x_{nj}$ is the random slope term in which γ_{nj} represents the random coefficient of variable x_n for the individual or group *j*; and γ_{0j} is the random intercept term, which represents the difference between the intercept for the individual or group *j* and the mean (global) intercept (Gillies et al. 2006). The GLM models were structured as logit models of the form:

$$g(x) = \ln\left[\frac{\pi(x)}{1-\pi(x)}\right] = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n \quad (2.3)$$

similar to the GLMM model but without the random slope and intercept terms (Manly et al. 2002). The resulting beta-coefficients (i.e., $\beta_1, \beta_2 \ldots \beta_n$) derived from the GLMM, or GLM for individual bears, became the coefficients for the RSFs.

I used a ratio of 10:1 available points per used point. For all the data, I removed points occurring in water or rare habitat types (mixed swamp, sand dunes, white spruce). Rare habitat types accounted for <0.4% of the study area. I omitted points falling outside the Saskatchewan Boreal Shield Ecozone, as there exists no data for those areas. Prior to modelling, I scaled the continuous variables, elevation and distance to linear features, by centering them and dividing by two standard deviations using the function scale from the package arm (Gelman and Su 2018) in R. I screened variables for collinearity using Pearson's correlation coefficients (Tabachnick et al. 2007). If two variables were collinear, I created two candidate models, each with one of the collinear terms dropped. I used habitat selection ratios to determine the reference category for

each model. The reference category was the habitat class with the selection ratio closest to one, indicating neither strong selection nor avoidance (Manly et al. 2002).

For each season and scale, I fitted five potential candidate models: global, quadratic, interaction, simple, and habitat only (Table 2.2). I used Akaike's information criteria (AIC) to determine the model that best fits the data. I performed k-fold cross validation on the top models to determine predictive power of the model (Boyce et al. 2002). I randomly split the data from each model by individuals into five folds (Roberts et al. 2017). Because each individual-bear model considers only one individual, blocking was not used in the k-fold cross validation. Instead, I split each individual's data randomly into five folds. I estimated Spearman-rank correlations (R_S) between ten bins of RSF scores and area-adjusted frequencies. A strong, positive R_S is indicative of a model with good predictive capacity (Boyce et al. 2002).

2.2.7 Comparing habitat selection between species

Caribou calves are most vulnerable to predation by black bears during their first four to six weeks of life (Bergerud 1971, Ballard et al. 1981, Pinard et al. 2012, Mahoney et al. 2016), therefore I focused my comparison of habitat selection to that time period. Caribou calving and post-calving seasons in my study area occur from May 1 – June 15 and June 16 – August 11, respectively (Superbie et al. 2019). To contrast the differences in habitat selection between black bears and caribou during the caribou calving and post-calving seasons, I employed latent selection difference (LSD). This method allows for direct comparison between two species or groups of interest. LSD uses the same equation as resource selection functions (equation 2.1), but $w(x)$ indicates the relative probability of one species (e.g. black bears; coded as 1) occurring on the landscape compared to another species (e.g. caribou; coded as 0). The selection coefficient (β_n) should be interpreted as relative difference in selection between bears and caribou, not selection of a habitat unit as is with RSFs (Latham et al. 2011). This model does not allow for individuals as random factors and therefore does not correct for unbalanced sampling design (Latham et al. 2011).

For the LSD models, I used the same covariates that were used in the species RSF analyses, which included habitat class, elevation, and distance to linear features (see section *2.2.5 Environmental covariates*). I obtained caribou use-availability data from calving and post-calving seasons from Superbie et al. (2019). The population study area for caribou was defined using 100% MCP around the individual home ranges. A key assumption is that all habitat types

should be equally available to both species within the study area (Latham et al. 2011). This assumption was not violated as I selected used points for caribou that overlapped with the black bear study area (Figure 2.1). I truncated the used points of the bears to match the beginning of the calving season and end of post-calving season (i.e. May 1 – August 11). I randomly selected one location per species per day for each season.

I cleaned and prepared the data for the LSD using the same methods for the RSF analyses. I removed points occurring in water or rare habitat types (mixed swamp, sand dunes, white spruce). I omitted points falling outside the Saskatchewan Boreal Shield Ecozone, as there exists no data for those areas. Prior to modelling, I scaled the continuous variables, elevation and distance to linear features, by centering them and dividing by two standard deviations using the function scale from the package arm (Gelman and Su 2018) in R. I screened variables for collinearity using Pearson's correlation coefficients (Tabachnick et al. 2007). If two variables were collinear, I created two candidate models, each with one of the collinear terms dropped. I used habitat selection ratios to determine the reference category for each model. The reference category was the habitat class with the relative selection ratio closest to one, indicating neutral relative difference in selection between species (Manly et al. 2002).

For each LSD, I fitted five potential candidate models: global, quadratic, interaction, simple, and habitat only (Table 2.2). I used AIC to determine the model that best fits the data. I calculated the relative operating characteristic curve (ROC) index to rate the probability that a model would correctly discriminate between one species and the other. ROC graphs plot the true positive rate, also called sensitivity, against the false positive rate, also called 1 - specificity (Swets 1988). The true positive rate is a measure of the proportion of sites at which the observations and predictions agree while the false positive rate is a measure of the proportion of disagreement between observations and predictions (Pearce and Ferrier 2000). Good model performance (i.e. high discrimination ability) is characterized by a curve that maximizes the true-positives while minimizing false-positives. Area under the curve (AUC) is calculated from the ROC where AUC values of 0.9 and above are indicative of high model accuracy, 0.7 to 0.9 good model accuracy, and less than 0.7 low model accuracy (Swets 1988).

2.2.8 Mapping habitat selection

To visualize the trends of the RSF and LSD analyses, I mapped the relative probabilities of selection of resource units (i.e., 30 × 30-m pixels) across the study area (Appendix E).

I generated RSF maps for each season and scale for both black bears and wolves and LSD maps for each species pair using raster layers of scaled elevation, scaled distance to linear features, and habitat classes (see section *2.2.5 Environmental covariates*). Continuous inputs were scaled using the formula:

$$(x - mean(x) \,/\, standard\ deviation(x)) \quad (2.4)$$

I generated maps using the Raster Calculator function in ArcGIS Desktop, v. 10.5 (ESRI, 2018), using the formula:

$$Exp((habitat\ raster) + [(\beta_8 * elevation\ raster) + (\beta_9 * elevation\ raster^2)] + [(\beta_{10} * distance\ to\ linear\ features\ raster) + (\beta_{11} * distance\ to\ linear\ features\ raster^2)] + (\beta_{12} * elevation\ raster * distance\ to\ linear\ features\ raster)) \quad (2.5)$$

where the habitat raster was altered to include the coefficients for each habitat class and the beta coefficients (β) for elevation and linear distance were entered manually for each season, scale, and species combination. I rescaled the resulting raster so the predicted RSF values were between zero and one using the formula:

$$(x - min(x))/(max(x) - min(x)) \quad (2.6)$$

2.3 Results

2.3.1 Seasonal habitat selection by black bears

Over the period of 2016–2018, 27 bears were collared. Of those 27 collars, 12 malfunctioned and went offline prematurely. Nine of the 27 collars were dropped prematurely or otherwise stationary without mortality confirmation. Six of the 27 bears were confirmed killed, five by hunters and one by vehicle collision. Points of use varied between seasons, scales, and number of individuals with available data. At the population scale, used points averaged 1553 ± 578 across seasons with a minimum of 1007 used points in the fall season (Table 2.3). At the home range scale, used points averaged 1464 ± 606 points across seasons with a minimum of 1007 points in the fall season (Table 2.3). At the individual level, used points averaged 153 ± 85 points per individual across all three seasons, with a minimum of 36 fixes from one bear in the fall season (Table 2.4).

Of the five candidate models estimated per season at the population scale, the global model had the lowest AIC value across all seasons and thus the highest support (Table 2.5). The

level of support for models was determined by the AIC values relative to the model with the lowest AIC. I selected the model with the lowest AIC but models within two ΔAIC represent models that are relatively equally supported and ΔAIC values greater than two have considerably less support (Burnham 2002). The global models included both quadratic and interaction terms for elevation and distance to linear features. At the home range scale for black bears, the top models were the global, quadratic, and habitat only models for the spring, summer, and fall seasons, respectively (Table 2.6). Most top models for the individual bear RSFs included elevation and linear distance, but inclusion of quadratic or interaction terms varied by individual (Table 2.7). All top models included individual animal ID as a random intercept.

Predictive ability of the population scale black bear model in spring was good with mean R_S = 0.90. Black bear models in summer and fall had poorer predictive ability: mean R_S was 0.41 and 0.28, respectively (Table 2.3). At the home range scale, the spring model had the top predictive ability between seasons, followed by summer then fall, but mean R_S per season was lower relative to the population scale (Table 2.3). Predictive ability of the individual bear models varied widely, R_S ranged from 0.88 to 0.31 across all individuals and seasons. No season had superior predictability and ranges of R_S within seasons were similar to the overall range (Table 2.4). For a season, the grand-mean R_S among individuals was 0.528, 0.740, and 0.676 for spring, summer, and fall, respectively. Mean R_S-values correlated with sample size (GPS-points) available to individuals in each season, which ranged from n = 36 to n = 283 (F = 9.31, P = 0.005, R^2 = 0.26).

In spring at the population level, black bears selected for mixed coniferous-deciduous forest stands and avoided black spruce swamp and mature black spruce habitats. In summer, bears selected for mixed coniferous-deciduous, open muskeg, and young-mid jack pine habitats. Bears did not significantly avoid any habitat type in summer. In fall, bears selected for mature black spruce, young-mid black spruce and young-mid jack pine (Table 2.8). At the population scale bears chose lower elevations in spring and summer but mid-high elevations in fall. Bears selected for linear features across all seasons at the population scale (Figure 2.3).

At the home range scale, bears selected for mixed coniferous-deciduous and avoided black spruce swamp in the spring. In summer season, bears selected for mixed coniferous-deciduous and young-mid jack pine stands and avoided mature black spruce and jack pine stands. Black bears selected for young-mid jack pine and avoided black spruce swamp in the fall

(Table 2.9). In spring and summer seasons, bears selected for lower elevations and lower distance from linear features (Figure 2.3).

Individual RSF analyses showed few habitat classes were significantly selected or avoided by individual bears. Black spruce swamp was avoided across all seasons by multiple individuals. Mixed coniferous-deciduous stands were selected for across all seasons by multiple individuals with the exception of one individual, who avoided these stands in summer. Young-mid jack pine was selected for by multiple individuals in summer and fall but was not significantly selected or avoided in spring. The remaining habitat classes were significantly selected or avoided by few individuals but remained the majority selectively neutral (Appendix B, Table B.1a-c). Individual bears varied in response to elevation (Figure 2.4). The majority of bears across seasons showed a slight bell curve with increasing selection for intermediate elevations. Few bears in spring showed relative selection for lower elevations. One bear showed the opposite of the bell curve in summer, with increasing relative probability of selection at lower and higher elevations. Another bear selected for higher elevations relative to lower elevations in the fall season. Individual bears generally selected lower distance to linear features in spring with the exception of two bears. Relative selection of linear features was highly variable in summer and fall seasons (Figure 2.5).

2.3.2 Comparing habitat selection between species

Points of use varied between seasons, scales, and number of individuals with available data. Analyses were run using n = 774 used points from 18 bears and n = 8525 points from 39 caribou (Table 2.10). Of the five candidate models estimated, the global model had the lowest AIC value and thus the highest support (Table 2.10). The global model included both quadratic and interaction terms for elevation and distance to linear features.

During the calving and post-calving seasons, bears were less likely to use black spruce swamps, open muskegs, and mature habitat classes compared to caribou. Bears were more likely to be found in mixed coniferous-deciduous stands compared to caribou (Table 2.11). Bears were slightly likelier to be found at lower elevations compared to caribou during the caribou calving and post-calving seasons. Bears selected lower distances to linear features compared to caribou (Figure 2.6). I evaluated the latent selection difference models using ROC and AUC. The models performed well appearing to correctly discriminate between one species and the other (Figure 2.7).

2.4 Discussion

2.4.1 Seasonal habitat selection by black bears

My study is the first to assess habitat selection for black bears in northern Saskatchewan. While the general habits of black bears are well understood, little research has been done on the species in the province and nothing has been applied, from a western scientific tradition, to the Boreal Shield, a unique region of boreal forest where anthropogenic impacts are low but fire disturbance is high. As generalist omnivores, black bear habitat selection can be linked to selection for certain food types as they become temporally available (Romain et al. 2013). Black bears tend to eat grasses, forbs, deciduous plants, and insects including ants during the spring and summer and switch to higher calorie soft- and hard-mast plants in the fall (Mosnier et al. 2008, Romain et al. 2013, Lesmerises et al. 2015). Their diet is often supplemented with opportunistic, higher-protein prey throughout the season (Robbins et al. 2007, Lesmerises et al. 2015, Popp et al. 2018). Short growing seasons in the boreal forest restrict the number of fruiting species and contribute to biophysical constraints responsible for the absence of fatty mast-producing species that are important for weight gain before denning in the fall (Reynolds-Hogland et al. 2007, Brodeur et al. 2008). Mosnier et al. (2008) found that black bears adapted to the low productivity of the boreal forest by consuming graminoids, especially in the spring.

Black bears in my study area were generally selecting for mixed coniferous-deciduous stands in the first half of the active season, but transitioned towards younger coniferous stands, usually jack pine, later in the active season. The mixed coniferous-deciduous habitat is relatively rare and patchily distributed across the landscape (Figure 2.8; 7% of the study area) so it likely provides some important habitat feature or food source that is important for the bears in this area. The distribution of a relatively important habitat type for black bears could contribute to the large home ranges observed in my study area (McLoughlin et al. 2019). Grasses are extremely rare in mixed coniferous-deciduous stands in my study area (McLaughlan et al. 2010). The mixed coniferous-deciduous habitat type offers a more open canopy that could favour alternate forbs and deciduous plants possibly important for bears in the spring and summer. During summer at the population scale, bears also relatively select for open muskeg habitats which could provide other graminoids (sedges) and berries (McLaughlan et al. 2010). The shift in relative selection towards young coniferous stands in the fall is not a surprise as bears rely heavily on berries to prepare for winter dormancy through much of North America (Nelson et al. 1983). In

my study area, velvet-leaved blueberry (*Vaccinium myrtilloides*) and lingonberry (*Vaccinium vitis-idaea*) were more commonly found and with equal or greater cover in young jack pine stands compared to mature stands, and generally, blueberry occurs more commonly in young jack pine stands than it does in any other stand (McLoughlin et al. 2019). Bears avoided black spruce swamp at both scales in spring and fall. Bogs have low abundances of forage plants for black bears (Mosnier et al. 2008, Latham et al. 2011). Black spruce swamp is a relatively open, wetland habitat that is selected for by caribou in my study area likely for its suspected refuge from predators (Latham et al. 2011, Superbie et al. 2019).

There was minimal difference in elevation across the available range to black bears (350 to 500 m). Mosnier et al. (2008) found that bears selected higher elevations in spring because little snow accumulation and earlier green-up and in autumn extended period of access to fruits. The range of elevation in my study area likely does not provide the same benefits of those study areas in mountainous or foothill regions. However, bears still slightly selected lower elevations at both scales in spring and summer. Conversely, bears selected higher elevations in the fall at the population scale. Black bears may use higher elevations in fall to extend the period during which they have access to fruits, following plant phenology (Raine and Kansas 1990); but I do not know the relationship between elevation and berry-producing plants in my study area.

Black bear selection for linear features at both population and home range scales in the study area could be indicative of use of linear features as travel routes to increase movement and search efficiency (Latham et al. 2011, Tigner et al. 2014, DeMars and Boutin 2018). In my study area, it is likely also heavily biased by the capture method: the commercial bait sites we used were located along the main highway for ease of access (Figure 2.1). Linear feature density across the range available to bears was still low (0.19 km/km^2) and this may limit the extrapolation of black bear response to linear features across the Boreal Shield in Saskatchewan, we can assume selection for linear features still holds true for the study population. However, it remains unknown what types of linear features the bears are using most in this study as linear features in my study were not separated by type. The main road intersecting most of the bears' home ranges is a relatively busy gravel highway but surrounding linear features include electrical utility corridors, fire breaks, survey cutlines, minor roads, and trails.

Black bears use relatively low-human-use linear features as travel corridors on the landscape with little risk to the individual (Tigner et al. 2014), and roads provide a mortality risk

associated with increased human presence and potential for vehicular collisions (Lodé 2000, Switalski and Nelson 2011). Roads are a primary source of mortality for black bears (Laufenberg et al. 2018, Wynn-Grant et al. 2018) so it is unsurprising that bears are found to avoid roads in some cases (Kasworm and Manley 1990). Roads are still used by black bears as travel corridors (Schwartz et al. 2010, Switalski and Nelson 2011) and could be why other studies have detected more frequent use of habitat near major highways and with increasing human influence and road densities (Apps 2006). Most importantly, temporal adjustment of road use has changed, black bears have been found to adjust active periods when near roads to avoid high levels of human activity (Schwartz et al. 2010). Human activity in my study area is low compared to other studies, therefore it is likely that many linear features available to the study individuals offer relatively low-risk for travel and foraging and may not provide the need to temporally adjust active periods. The main highway does present a significant mortality risk as we had one confirmed vehicle mortality of a bear whose home range spanned across the highway.

Multi-scale habitat selection studies are important as often selection patterns can vary between scales and therefore make it difficult to extrapolate trends between scales (Wiens 1989, DeCesare et al. 2012, Heisler et al. 2017). In my study area, black bear habitat selection did not differ greatly between population and home range scales with the exception of fall at the home range scale, where linear features and elevation did not play a strong role in habitat selection patterns (Figures E.1.1 – E.1.3). Under a hierarchy of habitat selection, bears should act to reduce predation (Creel et al. 2005, McLoughlin et al. 2005, Dinkins et al. 2014), competition (Wereszczuk and Zalewski 2015, Duquette et al. 2017), and human mortality risk (Basille et al. 2013, Stillfried et al. 2015) at broader scales but select for high quality forage at finer scales (Fortin et al. 2005, Boyce 2006). The lack of deviance in habitat selection patterns could indicate that broad scale selection pressures are still important at the home range scale. But given the low density and relatively short hunting season, perhaps broad scale selection pressures are less important and it is forage that becomes most limiting at broader scales. Smaller-scale analyses could extricate more valuable information regarding limiting factors to black bears in Saskatchewan.

Increasingly, researchers are understanding the need for assessing habitat selection patterns of individuals as patterns of selection at the population scale can often mask important patterns for individuals (Latham et al. 2011, Lesmerises and St-Laurent 2017). Individual

analysis is especially important for omnivorous and generalist species. Their ability to use a wide range of food sources and habitats allows them to exhibit behavioural plasticity in response to varying resources across the landscape (Lesmerises and St-Laurent 2017). Individual bears responded insignificantly to most of the habitat classes. When bears did show a significant selection or avoidance for a habitat class, it remained consistent across individuals and seasons, and was comparable to the population and home-range analyses, with a couple exceptions. Mixed coniferous-deciduous was still important to individuals across all seasons. Young-mid jack pine was also selected by individuals later in the active season. Black spruce swamp was avoided across all seasons by a few individuals. All three of these habitats showed similar trends at the population and home range scales. Conversely, black bear selection patterns at the individual level differed from the population and home range scale showing greater individual variation in response to elevation and linear features. In spring, the majority of bears selected for lower elevations consistent with drainages. Drainages such as rivers and streams can be used as natural linear features for travel across the landscape (Lyons et al. 2003). In summer and fall they generally selected for intermediate elevations although intermediate was relative to the elevation available across each individual home range. Variation in selection patterns for linear features could be a result of differences in linear feature types within each home range as different linear feature types are used differently by bears (Kasworm and Manley 1990, Apps et al. 2006, Tigner et al. 2014). Mortality risk associated with linear features can also vary between feature type as bears often avoid human activity associated with linear features rather than linear features themselves (Schwartz et al. 2010).

In some cases, lack of significant selection patterns for individual bears could be due to a result of their generalist, plastic behaviour leading to large variation within an individual's selection patterns. Low productivity of the boreal shield habitat means bears need to find food where they can and travel longer distances to acquire sufficient resources as habitat quality is the principal factor determining home range size (McLoughlin and Ferguson 2000). Spending time in a variety of habitats searching for a multitude of food sources can lead to blurry patterns of habitat selection. A similar variability and lack of clear pattern occurs with bear response to elevation and linear features. Individual bears diverge from the population and home range-level patterns seen in those models but the effect sizes are small. Variation in habitat selection can also be problematic when creating models to predict habitat selection.

Predictive ability of the population scale black bear model was best in spring and lowest in the fall as sample sizes (no. bears) declined; however, the same pattern of declining predictive ability as the seasons progressed from spring through fall was also reflected in RSF models at the home range scale. The latter occurred without an associated decline in animals. Because actual number of GPS used points per animal was similar between spring and fall, it is likely that the decrease in predictive ability reflected divergence in habitat selection patterns at the home range scale among bears as the year progressed. While it makes sense that given the generalist nature of bears, the predictive ability of the models can be weak, predictive capacity of the individual-level RSF models was a function of sample size.

2.4.2 Comparing habitat selection between species

The assessment of spatial overlap showed significant differences in selection by bears three of the seven habitat types relative to caribou during the calving and post-calving seasons. Caribou in my study area generally select for mature coniferous stands, treed bogs, and open muskegs and strongly avoided mixed coniferous-deciduous stands throughout the year (Superbie et al. 2019). During calving and post-calving seasons, caribou in my study area select for black spruce (*Picea mariana*) bogs and open muskegs (Superbie et al. 2019). Bears were significantly less likely to be found in caribou calving habitats, these results imply that boreal woodland caribou in the Boreal Shield of Saskatchewan maintain spatial separation from black bears during times of peak calf-vulnerability. Individual bears do not deviate significantly from this population-level trend and likely are not contributing significantly to caribou mortality and population dynamics in the area.

Moose calves are also vulnerable to predation by black bears during similar time frames as woodland caribou on the landscape (Saether et al. 1996, Garneau et al. 2008, McLaren et al. 2017). Studies of moose habitat selection during calving and post-calving time frames have found variable results including both selection and avoidance of forage availability and concealment cover, in addition to other important factors such as slope, elevation, and distance to water (Bowyer et al. 1999, Poole and Stuart-Smith 2005, Scarpitti et al. 2007, McLaren et al. 2017). Selection for conifer cover can provide spatial separation or concealment from predators but it does not provide high quality forage (Dussault et al. 2005, McGraw et al. 2012, McLaren et al. 2017). Alternatively, moose may prefer areas of higher forage quality but lower conifer cover, especially during peak lactation post-calving (Severud et al. 2019). Of the habitat classes

described in my study, mixed coniferous-deciduous habitat, especially young stands, likely provides the necessary cover and forage required by moose (Mabille et al. 2012), but more research is needed to confidently describe moose calving habitat in northern Saskatchewan. Bears selecting for mixed coniferous-deciduous stands early in the active season could overlap spatially with moose calves; however, given the combination of opportunistic carnivory in black bears and the low moose density in my study area, it is likely potential forage in the mixed stands that is driving black bear habitat selection.

The calving and post-calving seasons (calving: May 1 – June 15, post-calving: June 16 – August 11) coincide with the hunting season for black bears in the study area (April 15 – June 30). During the hunting season, active baits exist throughout the study area. Baiting activity occurs at locations accessible by vehicle and more remote locations only accessible by air or water. It is likely that every bear in the study area had regular access to bait during the hunting season. Baits become a reliable food source at a time when resources are scarce and can lead to consistent use by bears throughout the active baiting season. Consistent feeding at bait locations likely influences habitat selection during that time period. While baiting is legal across the majority of black bear range in Canada (Hristienko and McDonald 2007), it is not usually considered a factor in habitat selection studies. Similar baiting techniques are used as diversionary feeding to avoid conflicts with black bears during periods of food limitation (Ziegltrum 2004). Baits during the hunting season could act similarly, drawing bears away from their regular foraging to the reliable food source and potentially also away from foraging in areas where they may encounter caribou.

2.4.3 Conclusions

My study was the first to assess habitat selection patterns of black bears in the Boreal Shield of Saskatchewan. My results suggest that black bears in my study have very weak habitat selection patterns. As a generalist species, black bear patterns of habitat selection follow a gradient of forage availability. Black bears in my study area were generally selecting for mixed coniferous-deciduous stands in the first half of the active season, but transitioned towards younger coniferous stands, usually jack pine, later in the active season. Boreal Shield habitat has low productivity and provides little quality forage. A diet analysis would confirm what forage is most important to bears and the role supplied bait may play in a food limited landscape.

Black bears have been shown to be important predators of ungulate neonates across Canada. It has been suggested that bears might play a role in the decline of woodland caribou populations through calf predation. My results suggest that black bears spend the majority of their time foraging in mixed coniferous-deciduous habitat and avoiding calving habitat during critical periods of calf vulnerability. It is unlikely that black bears play a critical role in limiting caribou populations in the Boreal Shield of Saskatchewan based on their likely low density, and what my data suggest would be opportunistic encounters for caribou predation. Wolves are expected to be the main predator in this system. While managers may consider black bears among the suite of potential predators for caribou, actions aimed at increasing caribou productivity may better focus on wolf predation.

2.5 Tables and Figures

Table 2.1. Descriptions for the seven habitat classes used to characterize resource units (30 × 30-m pixels of land) in the Boreal Shield of Saskatchewan. Percent (%) area represents the percentage of land surface area (excluding water) covered by each habitat class within the Boreal Shield of Saskatchewan at the beginning of our study (May 2016). Canopy cover refers to the area of the ground in a site shaded by the canopy species. Note that the 0.38% of area unaccounted for is attributed to rare habitat classes not included in the models. Table adapted from Superbie et al. (2019).

Habitat class	% Area	Description
Mature jack pine	21.02	Canopy dominated by jack pine (*Pinus banksiana*) trees > 40 years old. Black spruce (*Picea mariana*) commonly co-occurs in small amounts (total canopy cover est. <15%).
Young-mid jack pine forest	36.54	Jack pine-dominated forests ≤ 40 years post-fire. These sites are expected to support fewer terrestrial lichens than sites dominated by mature jack pine forest.
Mature black spruce	8.38	Canopy dominated by black spruce forest > 40 years old. Terrestrial lichens comprise > 40% of the ground cover in some sites.
Young-mid black spruce forest	5.59	Black spruce-dominated forests ≤40 years post-fire. These sites are expected to support fewer terrestrial lichens than sites dominated by mature black spruce forest.
Mixed coniferous-deciduous	7.33	Either mixed deciduous forest comprised of trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) or mixed coniferous-deciduous forest comprised of black spruce trembling aspen and/or white birch. The overstory tends to be dense relative to the other habitat classes (total canopy cover est. > 48%).
Black spruce swamp	11.43	Somewhat open, black spruce-dominated canopy, generally comprised of mature trees (i.e., trees > 40-years old). Understory dominated by ericaceous shrubs. Terrestrial lichens comprise ~16% of ground cover.
Open muskeg	9.33	Lowland bog or fen habitats with generally low tree and shrub cover; some sites may support stands of tamarack trees (*Larix laricina*) or a dense clusters of shrubs, especially willow (*Salix* sp.) and river alder (*Alnus* sp.).

Table 2.2. Variables included in each of five mixed-effect logistic regression models used to assess habitat selection for black bears and wolves and compare habitat selection between aforementioned predators and boreal woodland caribou in the Boreal Shield of Saskatchewan.

Model	Variables
Global	Habitat + Elevation² × LinDist²
Quadratic	Habitat + Elevation² + LinDist²
Interaction	Habitat + Elevation × LinDist
Simple	Habitat + Elevation + LinDist
Habitat only	Habitat

Table 2.3. Sample size of GPS fixes (*n*) and number of individuals (*N*) used to develop generalized linear mixed models estimating seasonal resource selection at two scales for populations of black bears in the Boreal Shield of Saskatchewan and associated Spearman-rank correlation between ten Resource Selection Function (RSF) bins and area-adjusted frequencies for individually blocked five-fold (F1, F2, F3, F4, F5) cross validation. Mean represents the average Spearman-rank correlation of the five folds.

				Spearman- rank correlation					
Scale	Season	*n*	*N*	F1	F2	F3	F4	F5	Mean
Population	Spring	1493	18	0.960	0.963	0.985	0.997	0.578	0.897
	Summer	2159	11	0.079	0.988	0.921	0.976	-0.915	0.410
	Fall	1007	10	-0.733	0.839	0.891	0.219	0.176	0.278
Home range	Spring	1234	9	0.954	0.176	0.596	0.976	NA	0.675
	Summer	2152	10	0.055	0.827	0.061	0.927	0.830	0.540
	Fall	1007	10	0.200	0.100	0.700	-0.086	0.600	0.303

Table 2.4. Sample size of GPS fixes (*n*) used to develop generalized linear mixed models estimating seasonal resource selection of individual black bears in the Boreal Shield of Saskatchewan and associated Spearman-rank correlation between ten Resource Selection Function (RSF) bins and area-adjusted frequencies for individually blocked five-fold (F1, F2, F3, F4, F5) cross validation. Mean represents the average Spearman-rank correlation of the five folds.

			Spearman- rank correlation					
Season	Bear ID	*n*	F1	F2	F3	F4	F5	Mean
Spring	3002	52	0.661	0.397	0.245	0.254	0.378	0.387
	3007	118	0.713	-0.093	0.129	0.395	0.439	0.317
	3019	40	0.432	0.487	-0.315	0.519	0.404	0.305
	3022	168	0.542	0.697	0.603	0.287	0.111	0.448
	3023	172	0.453	0.966	0.415	0.683	0.850	0.673
	3029	153	0.775	0.800	0.671	0.799	0.912	0.791
	3031	174	0.806	0.693	0.543	0.349	0.854	0.649
	3039	162	0.448	0.713	0.558	0.202	0.580	0.500
	3053	195	0.872	0.530	0.551	0.806	0.650	0.682
Summer	3019	268	0.883	0.831	0.841	0.936	0.681	0.834
	3021	54	0.465	0.472	0.529	0.788	0.590	0.569
	3022	279	0.823	0.718	0.644	0.783	0.784	0.751
	3023	254	0.939	0.942	0.869	0.671	0.935	0.871
	3029	269	0.624	0.912	0.894	0.751	0.781	0.792
	3031	264	0.806	0.957	0.857	0.766	0.790	0.835
	3035	97	0.707	0.687	0.397	0.818	0.894	0.701
	3039	283	0.335	0.409	0.778	0.447	0.530	0.500
	3053	283	0.746	0.827	0.841	0.881	0.755	0.810
Fall	3002	36	0.898	0.847	-0.058	0.872	0.646	0.641
	3019	61	0.874	0.566	0.703	0.525	0.766	0.687
	3021	51	0.718	0.610	0.141	0.792	0.680	0.588
	3022	119	0.506	0.578	0.615	0.620	0.630	0.590
	3023	146	0.823	0.807	0.848	0.706	0.729	0.783
	3029	163	0.689	0.689	0.878	0.683	0.659	0.720
	3031	152	0.816	0.734	0.638	0.684	0.578	0.690
	3035	38	0.540	0.310	0.360	0.668	0.607	0.497
	3039	52	0.921	0.798	0.110	0.881	0.740	0.690
	3053	189	0.957	0.787	0.869	0.923	0.839	0.875

Note: k-fold not available for bear 3002 summer season as the top model was habitat only

Table 2.5. Comparison of models used to predict resource selection at the population scale for black bears in the Boreal Shield of Saskatchewan. Models are ranked based on Akaike's information criteria (AIC) values. ΔAIC measures the difference between each model and the top model and Akaike weights (w_i) indicates the probability that a model is best among an entire set of candidate models.

Season	Model	AIC	ΔAIC	w_i
Spring	Habitat + Elev² × LinDist² *	8306.3	0	1
	Habitat + Elev² + LinDist²	8336.6	30.3	<0.001
	Habitat + Elev × LinDist	8357.2	51	<0.001
	Habitat + Elev + LinDist	8372.7	66.4	<0.001
Summer	Habitat + Elev² × LinDist² *	12779.8	0	0.817
	Habitat + Elev² + LinDist²	12783.7	3.9	0.117
	Habitat + Elev × LinDist	12785.3	5.5	0.052
	Habitat + Elev + LinDist	12787.8	8.1	0.015
Fall	Habitat + Elev² × LinDist² *	5910.7	0	0.63
	Habitat + Elev × LinDist	5911.8	1	0.37
	Habitat + Elev² + LinDist²	5928.1	17.4	<0.001
	Habitat + Elev + LinDist	5930.2	19.5	<0.001

* Indicates top model

Table 2.6. Comparison of models used to predict resource selection at the home range scale for populations of black bears and wolves in the Boreal Shield of Saskatchewan. Models are ranked based on Akaike's information criteria (AIC) values. Delta AIC (ΔAIC) measures the difference between each model and the top model and Akaike weights (w_i) indicates the probability that a model is best among an entire set of candidate models.

Season	Model	AIC	ΔAIC	w_i
Spring	Habitat + Elev² × LinDist²	8043.2	0	1
	Habitat + Elev² + LinDist²	8063.6	20.4	<0.001
	Habitat + Elev × LinDist	8064	20.8	<0.001
	Habitat + Elev + LinDist	8092	48.8	<0.001
	Habitat	8247.9	204.7	<0.001
Summer	Habitat + Elev² + LinDist²	14253.5	0	0.448
	Habitat + Elev² × LinDist²	14254.5	1	0.268
	Habitat + Elev + LinDist	14255.1	1.6	0.202
	Habitat + Elev × LinDist	14256.9	3.4	0.082
	Habitat	14383.1	129.5	<0.001
Fall	Habitat	6571.3	0	0.573
	Habitat + Elev + LinDist	6573.9	2.5	0.16
	Habitat + Elev² + LinDist²	6574.1	2.8	0.142
	Habitat + Elev × LinDist	6575.6	4.3	0.067
	Habitat + Elev² × LinDist²	6575.9	4.6	0.058

Table 2.7. Summary of Akaike's information criteria (AIC) values and Akaike weights (w_i) of top models used to predict resource selection by individual black bears in the Boreal Shield of Saskatchewan. Akaike weights (w_i) indicates the probability that a model is best among an entire set of candidate models. Full dataset including other candidate models can be found in Appendix A.

Season	Bear	Model	AIC	w_i
Spring	3002	Habitat + Elev² + LinDist²	342.3	0.6503
	3007	Habitat + Elev² × LinDist²	768.6	0.638
	3019	Habitat + Elev + LinDist	266.1	0.529
	3022	Habitat + Elev² + LinDist²	1110.5	0.41
	3023	Habitat + Elev² × LinDist²	991.9	0.89
	3029	Habitat + Elev + LinDist	974.7	0.606
	3031	Habitat + Elev + LinDist	1121.8	0.36
	3039	Habitat + Elev² + LinDist²	1066.3	0.564
	3053	Habitat + Elev² + LinDist²	1215.6	0.7
Summer	3002	Habitat	670.6	0.532
	3019	Habitat + Elev² × LinDist²	1732.1	0.965
	3021	Habitat + Elev² × LinDist²	322	0.89
	3022	Habitat + Elev² × LinDist²	1829.1	0.56
	3023	Habitat + Elev² × LinDist²	1317.1	0.992
	3029	Habitat + Elev² × LinDist²	1755.3	0.7358
	3031	Habitat + Elev² + LinDist²	1643.7	0.73
	3035	Habitat + Elev² × LinDist²	627.8	0.828
	3039	Habitat + Elev² + LinDist²	1877.1	0.73
	3053	Habitat + Elev² × LinDist²	1854.8	0.961
Fall	3002	Habitat + Elev² + LinDist²	216	0.5464
	3019	Habitat + Elev² + LinDist²	350.2	0.704
	3021	Habitat + Elev² × LinDist²	317.5	0.62
	3022	Habitat + Elev² + LinDist²	745.9	0.58
	3023	Habitat + Elev² × LinDist²	898.7	0.9968
	3029	Habitat + Elev² × LinDist²	996.6	0.9985
	3031	Habitat + Elev² × LinDist²	933.2	0.88
	3035	Habitat + Elev² + LinDist²	228	0.64
	3039	Habitat + Elev² × LinDist²	297.5	0.52
	3053	Habitat + LinDist + LinDist²	1139.3	1

Table 2.8. Summary of beta coefficients (β) ± standard error (SE), and *p*-values (*P*) for generalized linear mixed models predicting seasonal resource selection at the population scale for a black bear population in the Boreal Shield of Saskatchewan.

	Spring				Summer				Fall			
Variable	β	SE	*P*		β	SE	*P*		β	SE	*P*	
Black Spruce Swamp	-0.382	0.135	0.005	*	0.044	0.104	0.670		-0.941	0.190	<0.001	*
Mature Black Spruce	-0.295	0.142	0.037	*	-3.227[a]	0.099	<0.001	*	0.405	0.194	0.036	*
Mature Jack Pine	-0.121	0.126	0.338		-0.109	0.102	0.285		-0.313	0.168	0.063	
Mixed Con-Dec	0.413	0.140	0.003	*	0.824	0.110	<0.001	*	-2.749	0.157	<0.001	*
Open Muskeg	0.108	0.133	0.416		0.249	0.106	0.019	*	-0.257	0.182	0.159	
Young-Mid Black Spruce	-3.389[a]	0.133	<0.001	*	0.153	0.127	0.231		0.655	0.183	<0.001	*
Young-Mid Jack Pine	-0.221	0.131	0.092		0.519	0.099	<0.001	*	1.029	0.156	<0.001	*
Elevation	-0.852	0.078	<0.001	*	-0.200	0.044	<0.001	*	0.180	0.053	<0.001	*
Elevation^2	-0.175	0.028	<0.001	*	-0.031	0.019	0.107		-0.058	0.028	0.037	*
LinDist	-2.397	0.108	<0.001	*	-1.624	0.055	<0.001	*	-1.109	0.063	<0.001	*
LinDist^2	0.283	0.081	<0.001	*	0.148	0.052	0.004	*	-0.047	0.064	0.458	
Elevation x LinDist	-0.520	0.095	<0.001	*	-0.139	0.057	0.016	*	0.307	0.070	<0.001	*

[a] Indicates reference habitat class for that season
* Indicates P≤0.05

Table 2.9. Summary of beta coefficients (β) ± standard error (SE), and *p*-values (*P*) for generalized linear mixed models predicting seasonal resource selection at the home range scale for a black bear population in the Boreal Shield of Saskatchewan.

	Spring				Summer				Fall			
Variable	β	SE	*P*		β	SE	P		β	SE	*P*	
Black Spruce Swamp	-0.306	0.111	0.006	*	-0.208	0.111	0.062		-0.655	0.175	0.000	*
Mature Black Spruce	0.048	0.126	0.703		-0.351	0.129	0.007	*	-2.465[a]	0.128	<0.001	*
Mature Jack Pine	0.167	0.104	0.108		-0.225	0.113	0.047	*	-0.115	0.146	0.432	
Mixed Con-Dec	0.348	0.124	0.005	*	0.249	0.115	0.030	*	-0.124	0.195	0.525	
Open Muskeg	-2.481[a]	0.094	<0.001	*	-0.048	0.113	0.667		-0.146	0.166	0.378	
Young-Mid Black Spruce	0.104	0.139	0.454		-2.278[a]	0.123	<0.001	*	0.328	0.170	0.054	
Young-Mid Jack Pine	-0.099	0.110	0.367		0.236	0.105	0.025	*	0.722	0.142	<0.001	*
Elevation	-0.403	0.068	0.000	*	-0.226	0.042	<0.001	*	NA	NA	NA	
Elevation²	-0.107	0.032	0.001	*	-0.025	0.025	0.313		NA	NA	NA	
LinDist	-0.693	0.057	<0.001	*	-0.358	0.040	<0.001	*	NA	NA	NA	
LinDist²	0.092	0.027	0.001	*	0.033	0.015	0.031	*	NA	NA	NA	
Elevation x LinDist	-0.255	0.057	0.000	*	NA	NA	NA		NA	NA	NA	

[a] Indicates reference habitat class for that season
* Indicates P≤0.05

Table 2.10. Comparison of latent selection difference (LSD) models used to compare resource selection during the calving and post-calving seasons between black bears and boreal woodland caribou in the Boreal Shield of Saskatchewan. Models were run using *n* fixes from each species of *N* individuals. Models are ranked based on Akaike's information criteria (AIC) values. Delta AIC (ΔAIC) measures the difference between each model and the top model and Akaike weights (w_i) indicates the probability that a model is best among an entire set of candidate models.

Species	*n*	*N*	Model	AIC	ΔAIC	df	w_i
Bear	774	18	Habitat + Elev² × LinDist²	3268	0	12	0.9953
			Habitat + Elev² + LinDist²	3278.7	10.7	11	0.0047
Caribou	8525	39	Habitat + Elev × LinDist	3319.4	51.4	10	<0.001
			Habitat + Elev + LinDist	3332.3	64.2	9	<0.001
			Habitat	5086	1818	7	<0.001

Table 2.11. Summary of beta coefficients (β) ± standard error (SE), and *p*-values (*P*) for latent selection difference (LSD) models comparing resource selection during the calving and post-calving seasons for black bears and boreal woodland caribou in the Boreal Shield of Saskatchewan.

	BearCaribou			
Variable	β	SE	*P*	
Black Spruce Swamp	-0.851	0.157	<0.001	*
Mature Black Spruce	-0.478	0.187	0.011	*
Mature Jack Pine	-0.471	0.157	0.003	*
Mixed Con-Dec	2.269	0.236	<0.001	*
Open Muskeg	-0.513	0.161	0.001	*
Young-Mid Black Spruce	0.299	0.215	0.165	
Young-Mid Jack Pine	-4.457	0.176	<0.001	*
Elevation	-0.755	0.131	<0.001	*
Elevation²	-0.092	0.046	0.046	*
LinDist	-2.840	0.117	<0.001	*
LinDist²	0.726	0.060	<0.001	*
Elevation x LinDist	-0.451	0.130	<0.001	*

[a] Indicates reference habitat class for that season

* Indicates P≤0.05

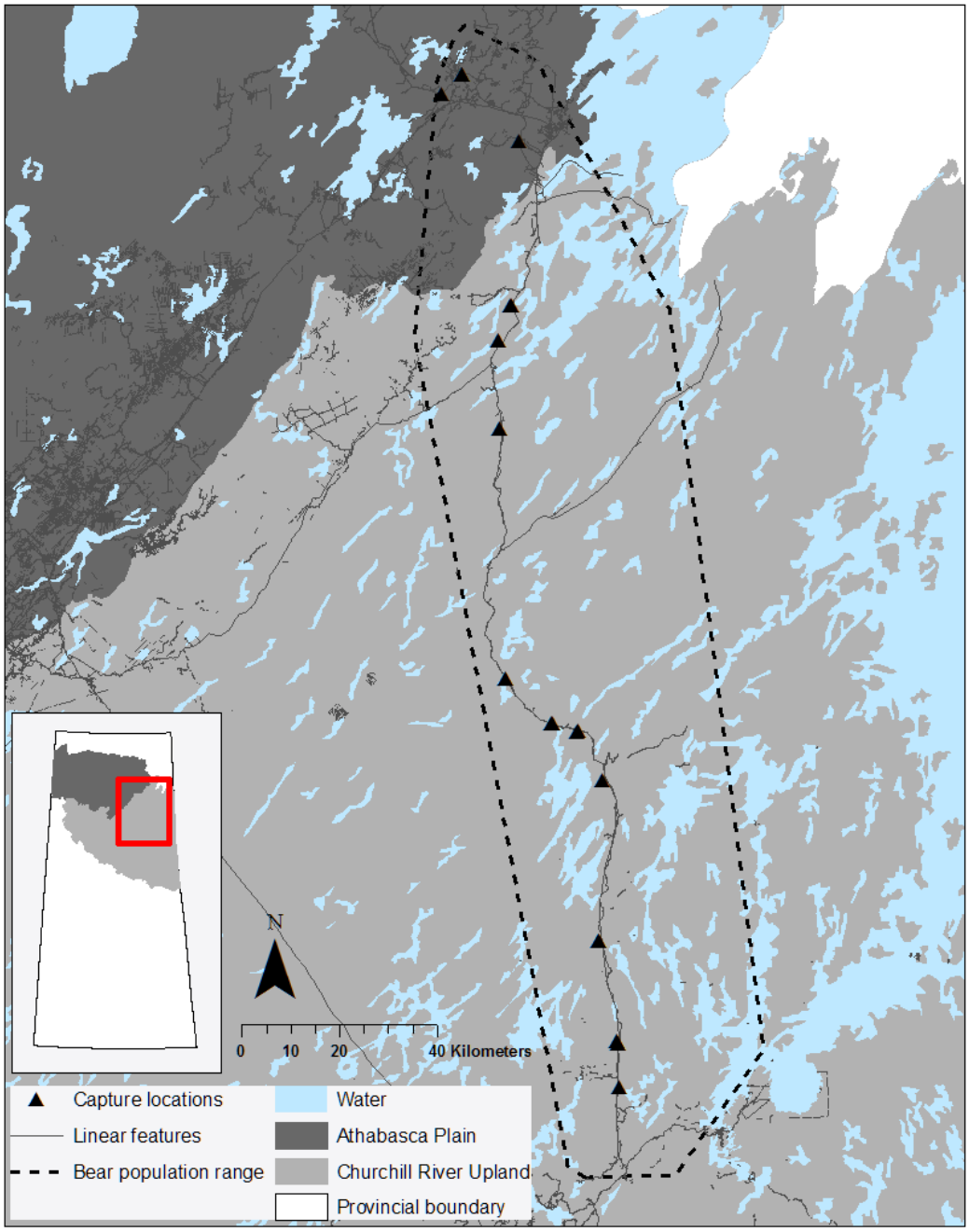

Figure 2.1. Capture locations, and linear features within the study area for black bears in the Boreal Shield of Saskatchewan. The study area for black bears and wolves was defined as the 100% minimum convex polygon (MCP) around all GPS fixes for each species, excluding dispersers.

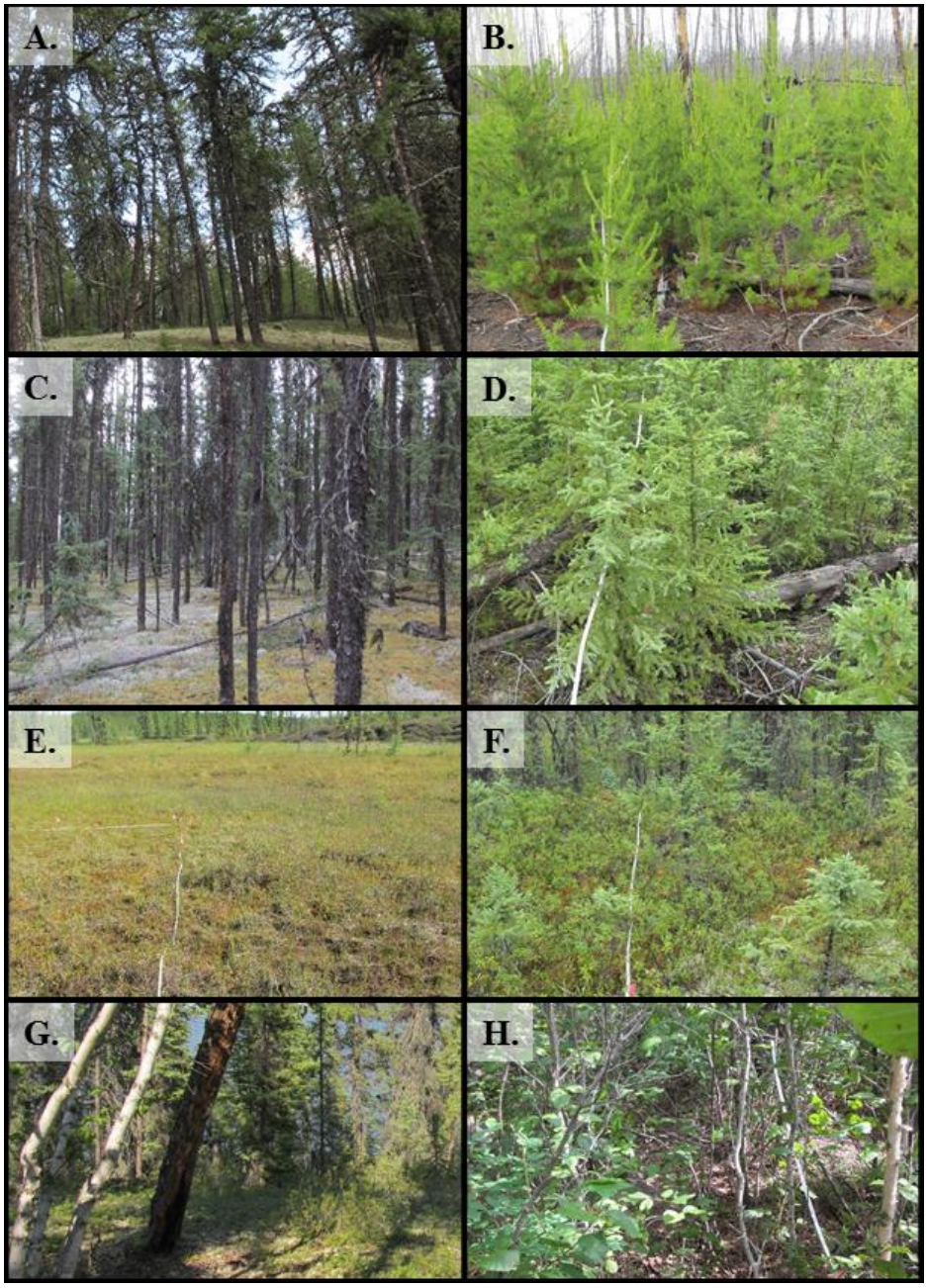

Figure 2.2. Images of the seven habitat classes used to characterize the environment and model resource selection by black bears in the Boreal Shield of Saskatchewan. A. Mature (> 40 years) jack pine forest; B. Early successional (≤ 40 years) jack pine forest; C. Mature black spruce forest; D. Early successional black spruce forests; E. Open muskeg; F. Black spruce swamp; F. Mixed coniferous-deciduous forests; H. Early successional deciduous forests. Habitat G and H were pooled for analysis. Photo credit: Ruth Greuel. Figure adapted from McLoughlin et al. 2019.

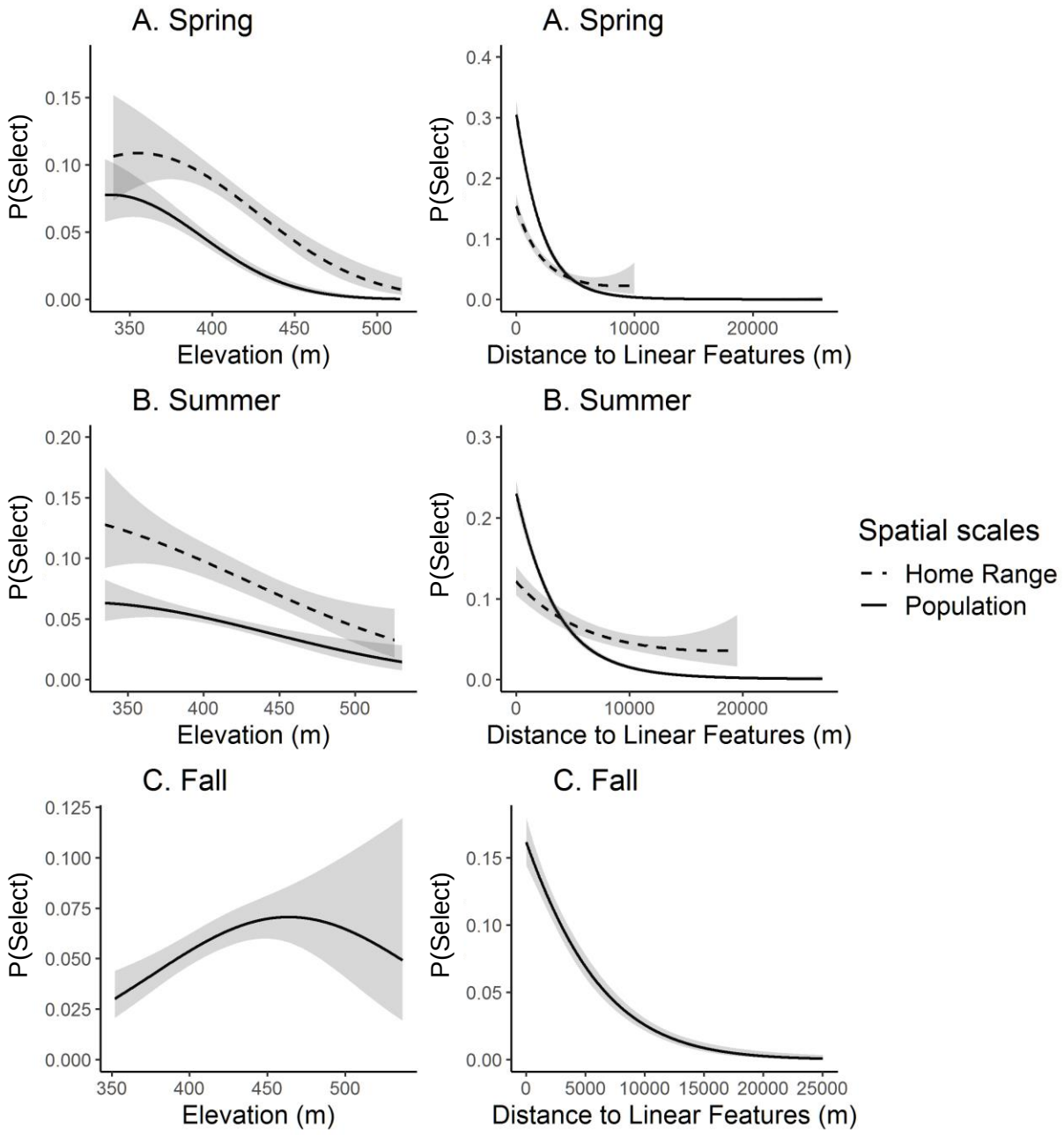

Figure 2.3. Plot of the predicted relative probability of selection (P(Select)) by black bears in the Boreal Shield of Saskatchewan as a function of the scaled (centered by the mean and divided by standard deviation) elevation and distance to linear features derived from the top model for each season and spatial scale. Solid lines represent the population scale and dashed lines represent the home range scale. The top fall model at the home range scale does not include elevation or distance to linear features.

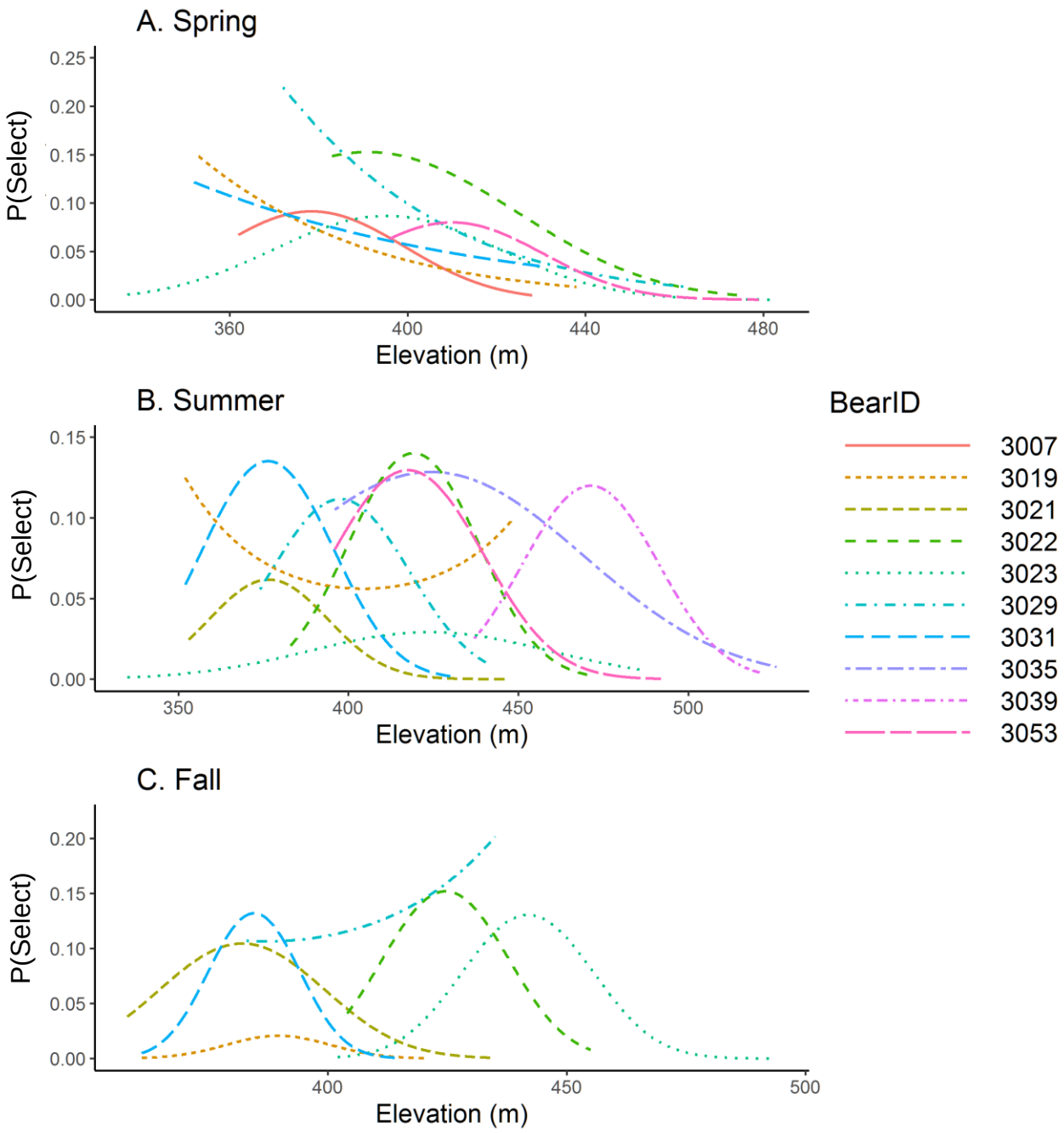

Figure 2.4. Plot of the predicted relative probability of selection (P(Select)) by individual black bears in the Boreal Shield of Saskatchewan as a function of the scaled (centered by the mean and divided by standard deviation) elevation derived from the top model for each season. Each line corresponds to an individual bear.

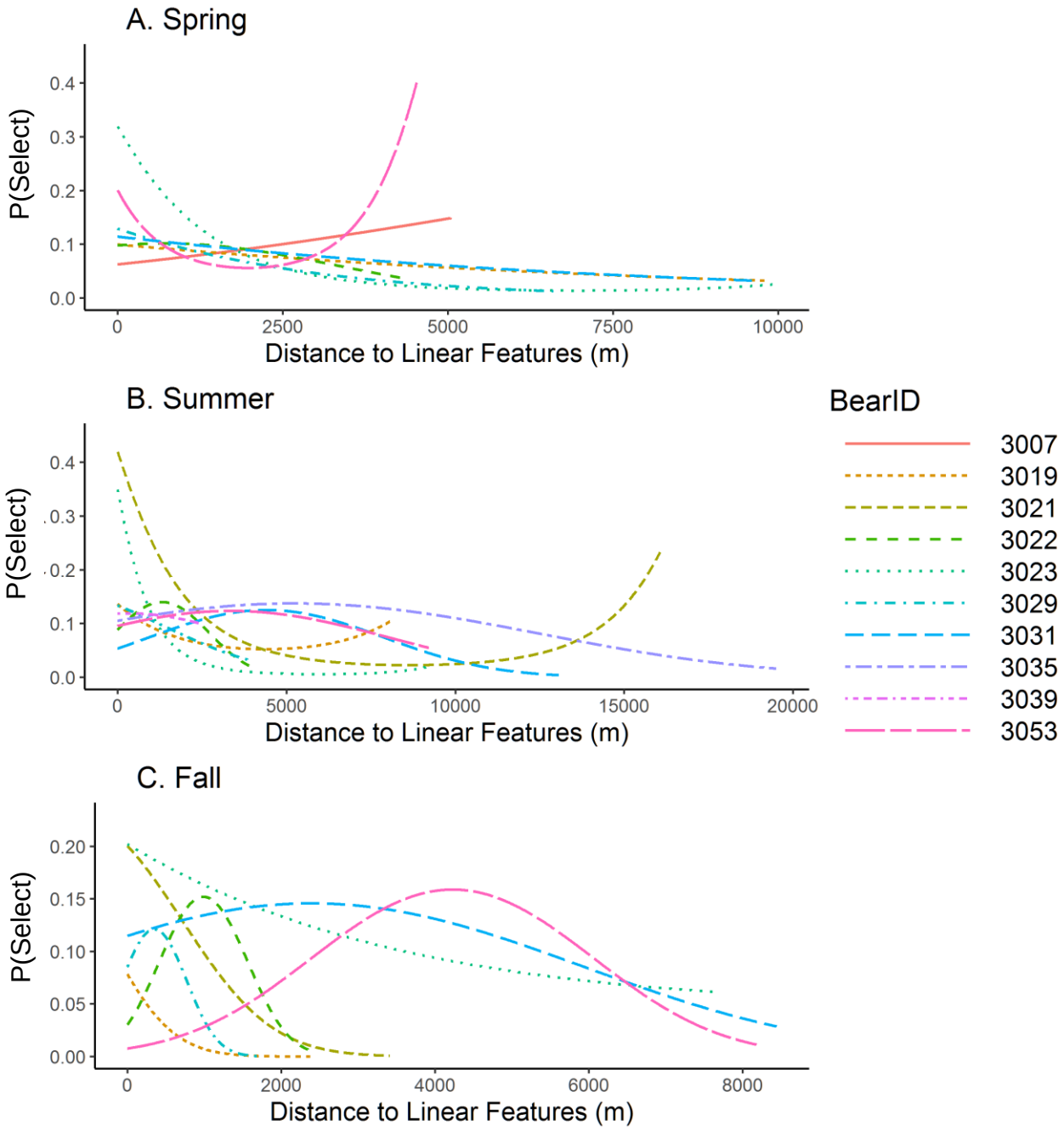

Figure 2.5. Plot of the predicted relative probability of selection (P(Select)) by individual black bears in the Boreal Shield of Saskatchewan as a function of the scaled (centered by the mean and divided by standard deviation) distance to linear features derived from the top model for each season. Each line corresponds to an individual bear.

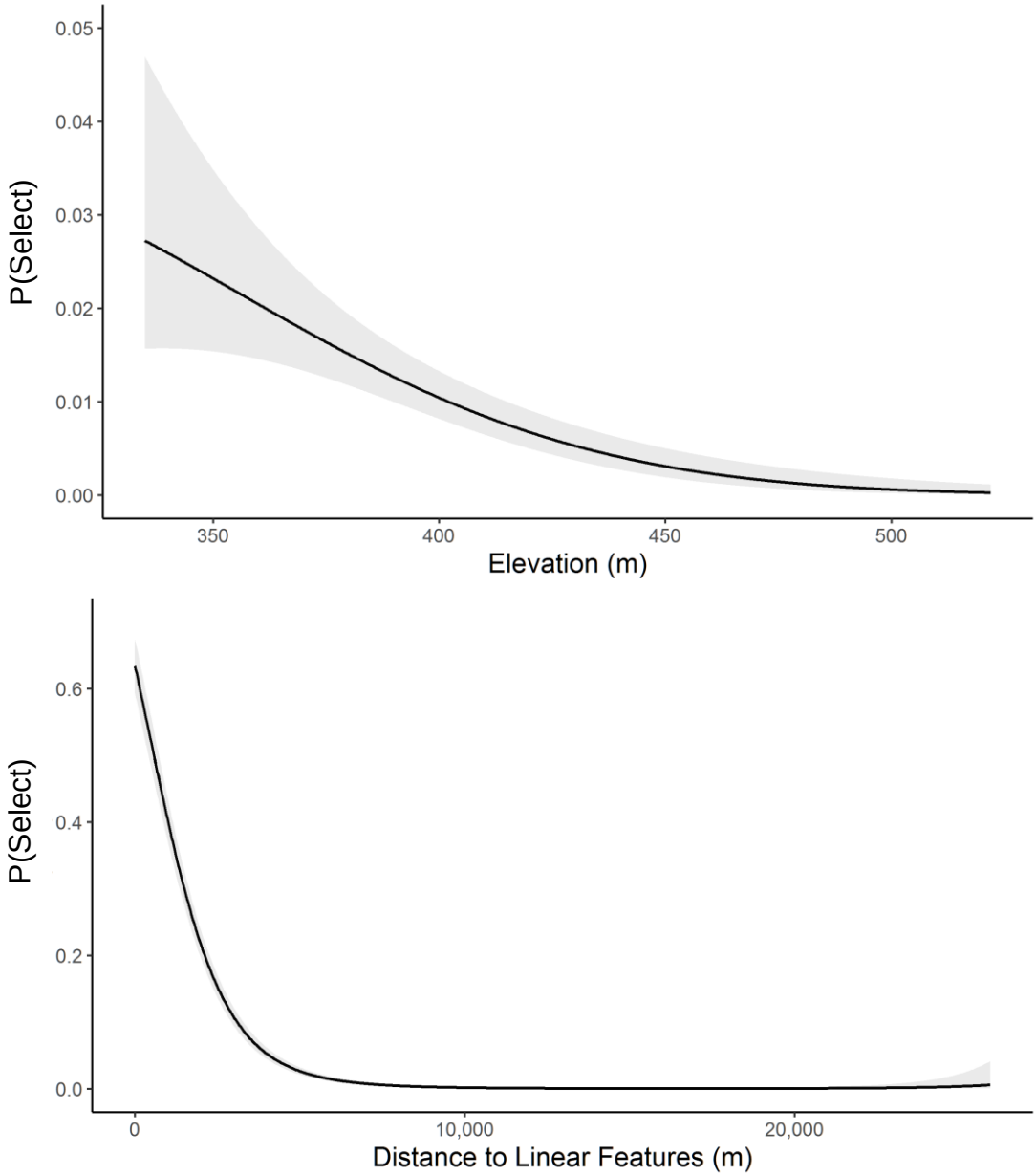

Figure 2.6. Plot of the predicted relative probability of selection (P(Select)) of a resource unit by black bears compared to boreal woodland caribou during the caribou calving and post-calving seasons in the Boreal Shield of Saskatchewan as a function of the scaled (centered by the mean and divided by standard deviation) elevation and distance to linear features derived from the top model.

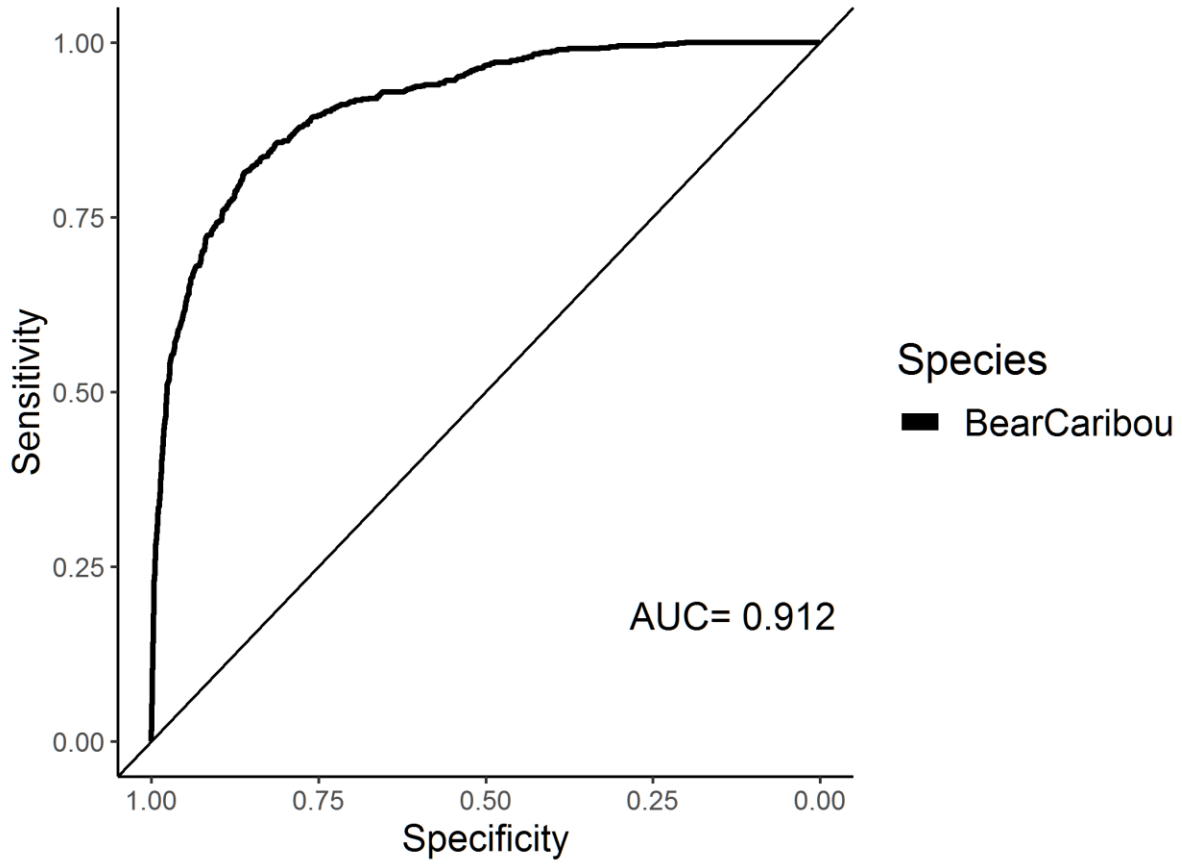

Figure 2.7. Relative operating characteristic curves (ROC) and area under the curve (AUC) for the latent selection difference (LSD) model attempting to assess differential habitat selection of black bears and boreal woodland caribou in the Boreal Shield of Saskatchewan. The straight line represents the case where AUC = 0.5 and the model has no discrimination capacity.

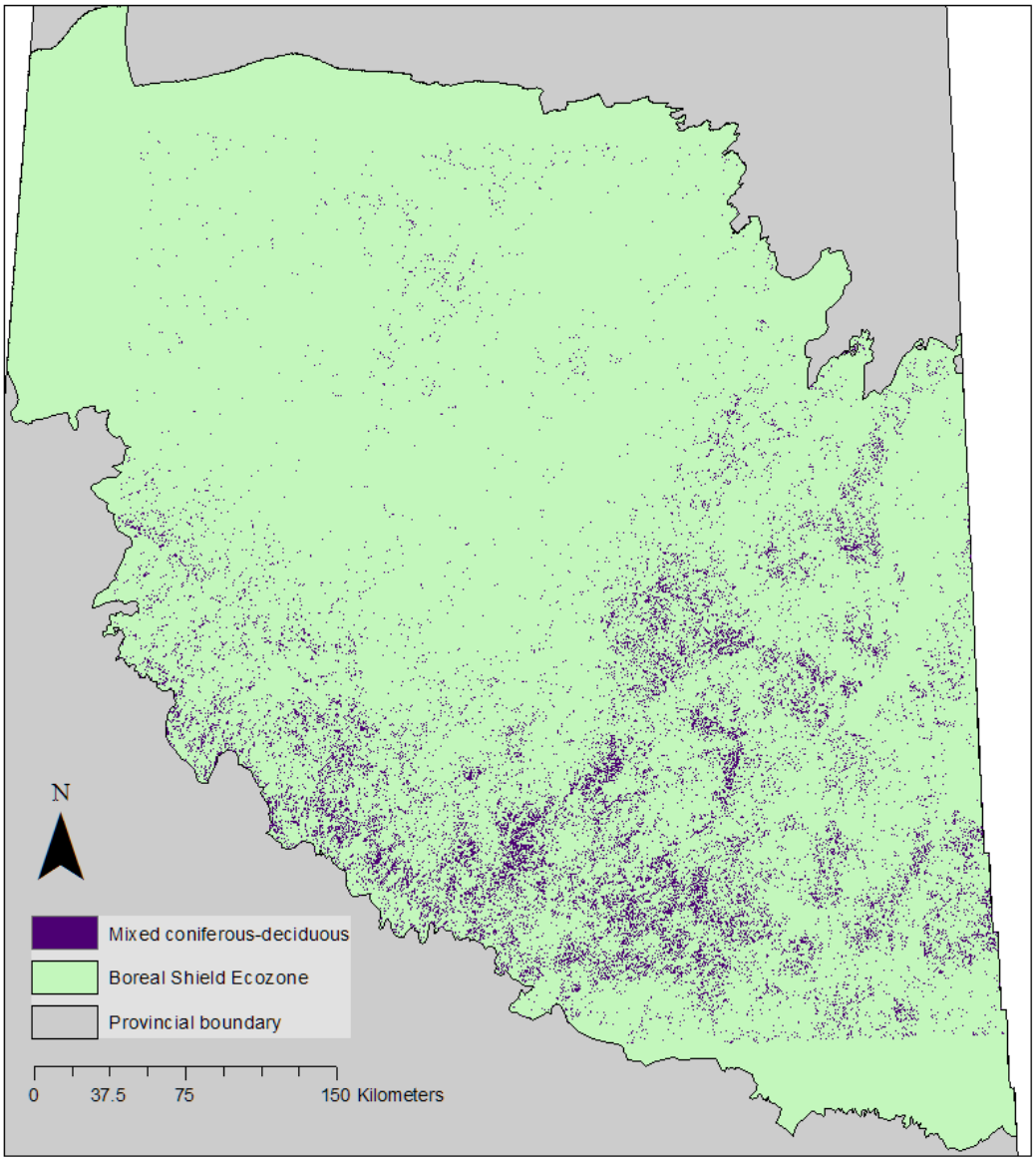

Figure 2.8. Availability of mixed coniferous-deciduous habitat across the Boreal Shield of Saskatchewan.

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CHAPTER 3: HABITAT SELECTION BY GRAY WOLVES IN THE BOREAL SHIELD OF SASKATCHEWAN

3.1 Introduction

Predator-prey dynamics are an important driver of habitat selection (Sih 2005). Habitat selection by both predators and prey are dynamic processes where each responds to one another, tempered by environmental factors, in a complex behavioural interaction (Lima 2002, Sih 2005). Predators often select habitat following abundance of prey or prey habitats. But disturbance by humans and human activity can influence habitat selection through similar mechanisms as predator-prey interactions (Frid and Dill 2002, Oriol-Cotterill et al. 2015).

In forested landscapes, linear features are a common human disturbance, including roads, railways, trails, power lines, pipelines, and seismic lines (Dawson et al. 2018). Linear features are known to affect predator-prey dynamics but the outcome can be unpredictable (Tablado and Jenni 2017). One of the most well-known examples of the impact of linear features is on the interactions between wolves (*Canis lupus*) and woodland caribou (*Rangifer tarandus caribou*). In human disturbed landscapes, linear features are thought to be an important factor in the decline of threatened woodland caribou by influencing the rate at which predators encounter and kill caribou (Paquet et al. 2010, Latham et al. 2011b, Latham et al. 2011c, Whittington et al. 2011, DeMars and Boutin 2018). Ehlers et al. (2014) found wolves move a reduced speeds and exhibit more undirected movements typical of prey searching and hunting when near to disturbance features. Other studies have demonstrated that wolves have increased movement rates and linear travel in areas with disturbance features (McKenzie et al. 2012, Ehlers et al. 2014, Dickie et al. 2017). Increased movement rates could function to reduce encounters with humans, increase encounter rates with prey, or facilitate territory monitoring (McKenzie et al. 2012, Ehlers et al. 2014, Dickie et al. 2017). Wolves have also been found to alter selection for linear features as a function of linear feature density (habitat functional response; Mysterud and Ims 1998). Generally, wolves are more likely to select for disturbance features in areas with higher disturbance feature density (Hebblewhite and Merrill 2008, Newton et al. 2017) but the

strength and direction of responses can vary between seasons, linear feature types, or study populations (Houle et al. 2010, DeMars and Boutin 2018).

Human disturbance can also impact predator-prey interactions through habitat mediated apparent competition, a form of apparent competition (Holt 1977). In the case of woodland caribou, habitat mediated apparent competition happens when human disturbance leads to an increased occurrence of early seral stage habitats on the landscape; these habitats support an increased number of moose (*Alces alces*) and deer (*Odocoileus* sp.), which in turn causes wolves to follow. The end result being a disproportionately high mortality of secondary prey such as woodland caribou (Seip 1992, Wittmer et al. 2005).

The predator-prey relationship between caribou and wolves is relatively well studied across Canada in highly modified landscapes where forestry and the oil and gas industry contribute most to disturbance in the area relative to natural disturbance such as fire (Environment Canada 2012). Yet, the majority of the extant boreal caribou range in Canada occurs in areas affected by more natural disturbance than industrial (McLoughlin et al. 2019). In the Boreal Shield of Saskatchewan, there exists low anthropogenic disturbance and high levels of fire disturbance. Less than 3% of the area occurs within 500 meters of industrial features (e.g. roads, transmission lines, settlements, mines), but over 55% of the area has been mapped as burned in the last 40 years (Parisien et al. 2004). Linear features exist at a low density of 0.14 km of lines per square kilometer across my study area. The Saskatchewan Boreal Shield stands out as a relatively natural ecosystem: all of the expected predators (e.g., wolves, black bears [*Ursus americanus*]) and prey (caribou, moose, beaver [*Castor Canadensis*]) occur, but without the invasive species that can exacerbate predation pressure (e.g., coyotes [*Canis latrans*], white-tailed deer [*Odocoileus virginianus*]) known from more southern ranges (McLoughlin et al. 2019). Even with high amounts of fire disturbance in the Boreal Shield of Saskatchewan, moose and wolf densities are remaining low, caribou densities are remaining high, and therefore it is unlikely that habitat mediated apparent competition is occurring in this fire-disturbed landscape to the same effect it occurs in more human-disturbed landscapes (Neufeld et al. 2019). In fact, caribou may be more important to wolves than are moose in the Boreal Shield of Saskatchewan (Neufeld et al. 2019).

I did not know how wolves would select habitat in response to the habitat conditions and exceptionally limited extent of linear features in the Saskatchewan Boreal Shield. This aspect of

wolf ecology has never been addressed at the levels of anthropogenic disturbance observed in our study area, anywhere in North America (McLoughlin et al. 2019). The purpose of this study is to fill in the aforementioned gaps by assessing habitat selection of wolves in a high-fire, low-human disturbance landscape and comparing that to what we know about habitat selection of caribou (Superbie et al. 2019) in the Boreal Shield of Saskatchewan. I assessed habitat selection of wolves across seasons delineated based on changes in movement, and at two spatial scales: within the range of the study population (the "population scale") and within individual home ranges (the "home range scale"). However, the population-level analyses of generalist species, such as wolves, can mask the impact and preferences of individuals (Boyce et al. 2003, Urton and Hobson 2005, Lesmerises and St-Laurent 2017). Therefore, I also analyzed individual habitat selection patterns for each wolf at the home range scale.

If caribou are the most important ungulate to wolves in our study area, then we should find habitat selection of wolves to track that of woodland caribou in the same area as prey habitat drive selection patterns of wolves (Courbin et al. 2014, Kittle et al. 2017). Caribou generally select for mature coniferous stands, treed bogs, and open muskegs throughout the year (Superbie et al. 2019). Caribou can use habitat selection as an anti-predator tactic, especially during calving, to separate from predators (Bergerud et al. 1984). Caribou of the Boreal Shield of Saskatchewan select for black spruce (*Picea mariana*) swamps and open muskegs during calving and post-calving seasons (Superbie et al. 2019). Forested wetlands can offer refuge from black bears, which are important predators of calves (Latham et al. 2011a). But open muskegs may appeal to moose, alternate prey to wolves (Timmermann and McNicol 1988, Shipley 2010), and therefore represent a tradeoff between predation risk from wolves and bears (Leblond et al. 2016).

To compare habitat selection between species, I used latent selection difference (LSD; Mueller et al. 2004, Latham et al. 2011a) to identify the potential for wolf-caribou and wolf-bear habitat selection overlap during the calving and post-calving periods. As shown in Chapter 2, black bears and caribou in our study area show little overlap in habitat selection during the calving season indicating that bears are not a major threat to consider. If caribou are successfully avoiding bears during the calving season, they may be faced with increased predation risk from wolves during that time (predator facilitation); therefore I would expect to see greater overlap in habitat selection between wolves and caribou during the calving season. Conversely, if caribou

are simultaneously avoiding both predators during calving (predator avoidance), then I would expect to see less overlap in habitat selection between wolves and caribou during the calving season. Wolves may show a functional response to linear features, disproportionately increasing or decreasing their use only as they increase in density on the landscape, but we may not see a response of wolves to linear features at the low densities observed in my study area.

3.2 Methods

3.2.1 Study area

The broader study area was delimited by the borders of the Boreal Shield Ecozone of northern Saskatchewan, Canada (Figure 3.1). The population study area for wolves was defined using 100% minimum convex polygon (MCP) each around cleaned GPS fixes (n = 37,028) for wolves, excluding dispersers. The Boreal Shield of Saskatchewan includes two main ecoregions: Churchill River Upland and Athabasca Plains. The Churchill River Upland is composed of Precambrian Canadian Shield bedrock with rocky outcrops and high relief (Padbury et al. 1998).The Churchill River Upland is characterized by continuous stands of jack pine and black spruce, as well as smaller areas of mixed forests comprised of black spruce interspersed with trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), balsam poplar (*Populus balsamifera*) and/or tamarack (*Larix laricina*). The Athabasca Plains Ecoregion is flatter and mainly composed of networks of sandy glacial deposits, moraines and eskers and is characterized by continuous jack pine forest (Secoy 2006). Overall, the region is relatively dry with long, cold winters and little snow, and short growing seasons (Padbury et al. 1998). Over 90% of the Boreal Shield Ecozone was coniferous forest of varying stand age; mixed and deciduous forests were rare (7% area; Table 3.1). The topography of the area is rolling with numerous lakes and wetlands. Elevation averaged 440 ± 70 m, higher elevations occurred in the western half of the Ecozone. The elevation available to wolves ranged from 300 to 600 m. At the time of study commencement, total human disturbance (e.g., roads, mines, transmission lines) was extremely low in the study area (0.18% of total area; linear features at 0.14 km of lines per km^2 across the combined study area) but fire disturbance was high (46.98% of landmass being burned in the last 40 years; McLoughlin et al. 2019).

3.2.2 Capture and collaring of wolves

In March 2014, we deployed 26 Lotek Iridium® Track M 2D GPS collars on wolves in the study area. In collaboration with Bighorn Helicopters Inc. (Cranbrook, British Columbia, Canada), wolves were physically immobilized by net gun following Animal Use Protocol 20130127 of the University of Saskatchewan and permit 14FW037 of the Saskatchewan Ministry of the Environment. In March 2015, an additional 12 wolves were captured in the study area and fitted with the same collars by the same methods as the previous year. In total 37 wolves occupying 18 suspected packs were collared. All collars were programmed to fix locations every three hours and to automatically release after four years.

3.2.3 Defining seasons for wolves

When movement rates of animals change non-linearly over time, increases or decreases in movement rate, specifically local maxima and minima, can be used to define the temporal limits of seasons for animal populations (van Beest et al. 2013). I estimated seasonal boundary dates using a generalized additive mixed model (GAMM) for wolves (n = 9). I omitted individual wolves that did not survive a full 365 days over the two-year monitoring period (March 2014 – March 2016) or wolves that had long migrations outside of the study area. I fit log-transformed daily movement rate (m/hr/day) as the response variable and day of the year (1-365) and the smoothing function using library gamm4 (Wood and Scheipl 2017) implemented in R statistical software (R Core Team 2018). To account for the hierarchical sampling design (i.e., relocations nested within individuals), I included animal ID as a random intercept. I used a cyclic cubic regression spline, with the optimal curve estimated by generalized cross-validation (Wood 2017). To find the local maxima and minima of this curve, I identified the second derivatives of the model smoother.

3.2.4 Spatial scales of resource selection

Habitat selection can also vary across spatiotemporal scales; to capture such variation it is important to examine selection over multiple spatiotemporal scales (Boyce et al. 2003). For analysis of resource selection, I defined habitat availability to wolves at two spatial scales within each season. At the population scale, I defined availability as the 100% MCP around all of the GPS locations of wolves. I truncated MCPs at the boundary of the Boreal Shield Ecozone in Saskatchewan due to a lack of environmental data for areas outside said boundaries.

For the home range scale, I defined availability for individual wolves using the 95% weighted autocorrelated kernel density estimate (AKDE) available in the ctmm (continuous-time movement modelling) package (Version 0.5.3, Calabrese et al. 2016) using R statistical software (R Core Team, 2018). This method explicitly accounts for spatiotemporal autocorrelation in telemetry data by calculating an appropriate smoother bandwidth given the data and an autocorrelated movement model. I used a fitted Ornstein-Uhlenbeck-F (OUF) motion model using initial model parameters obtained from visualizing the auto-correlation structure in an empirical variogram of the telemetry data (Fleming et al. 2014). I also truncated individual home ranges at the Saskatchewan Boreal Shield Ecozone boundaries. I calculated AKDEs for wolves who had nine months of fixes. AKDEs were discarded if the variogram did not asymptote meaning the wolf was not monitored long enough to be able to account for spatiotemporal autocorrelation in the data. Individuals who showed movement patterns indicative of dispersal, or patterns I was unable to confidently characterize, were not considered in calculating AKDEs. For the individual wolf analyses, I defined availability using the same methods as the home range scale analyses (95% AKDE).

3.2.5 Environmental covariates

I described the environment within the study area in terms of resource units defined as 30 × 30-m pixels characterized by: elevation (m), proximity to linear features in m (e.g., major roads, trails, geophysical survey lines, fire breaks, transmission lines, etc.), and habitat type (n = 7; Table 3.1, Figure 3.2). Elevation information as extracted from a raster layer (resolution = 30 × 30-m) derived from a digital elevation model in ArcGIS Desktop, v. 10.5 (ESRI, 2018). I measured the proximity to a linear feature as the Euclidean distance (m) between a point location and the edge of the closest linear feature. The habitat classes were derived from a raster layer of 27 Forest Ecosite Classes (FECs). The FECs were grouped and retained according to specific habitat features relevant to boreal woodland caribou (see Stewart 2016). The vegetation raster was updated each year with wildfire data to account for changes in forest stand age. The age threshold between the early-successional and mature forests was 40 years post-fire, chosen for expected recovery time for forage lichens for caribou (Environment Canada 2012, Stewart 2016).

3.2.6 Seasonal habitat selection by wolves

Resource selection functions (RSFs) are functions that are proportional to the probability of selection of a defined resource unit (Lele et al. 2013). Species interactions, including predator-prey, can be modelled using RSFs (Hebblewhite et al. 2005). RSF values are defined by the following log-linear equation (Manly et al. 2002):

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_n x_n) \quad (3.1)$$

where *w(x)* is the relative probability of selection; $\beta_1, \beta_2, \ldots \beta_n$ are the selection coefficients (i.e. slopes) based on the variables, $x_1, x_2, \ldots x_n$.

For each season and scale, I generated RSFs using logistic regression to compare environmental attributes (see section *3.2.5 Environmental covariates*) of used locations (GPS locations of wolves) to a set of randomly sampled locations (i.e. available points) within the ranges of wolves. To account for hierarchical telemetry data (i.e., relocations are nested within individual animals), I used generalized linear mixed models (GLMMs) in the lme4 package (Version 1.1-18-1, Bates et al. 2014) in R statistical software, with presence/availability as the response and animal ID as a random intercept (Gillies et al. 2006). In the case of the individual wolf RSFs, a generalized linear model (GLM) was fit in place of the GLMM as each model only considered one individual and therefore it was unnecessary to include animal ID as a random intercept. GLMMs were structured as logit models of the form:

$$g(x) = \ln\left[\frac{\pi(x)}{1-\pi(x)}\right] = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n + \gamma_{nj} x_{nj} + \gamma_{0j} \quad (3.2)$$

where $g(x)$ is a binomial response comparing the set of animal relocations (i.e., used points) to the set of randomly sampled locations (i.e., available points); ln [$\pi(x)$/1- $\pi(x)$] is the logit-link function relating the binomial response to the linear predictor on the right side of the equation; β_0 is the global intercept; $\beta_1, \beta_2 \ldots \beta_n$ are the beta-coefficients for the covariates $x_1, x_2 \ldots x_n$; $\gamma_{nj} x_{nj}$ is the random slope term in which γ_{nj} represents the random coefficient of variable x_n for the individual or group *j*; and γ_{0j} is the random intercept term, which represents the difference between the intercept for the individual or group *j* and the mean (global) intercept (Gillies et al. 2006). The GLM models were structured as logit models of the form:

$$g(x) = \ln\left[\frac{\pi(x)}{1-\pi(x)}\right] = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n \quad (3.3)$$

similar to the GLMM model but without the random slope and intercept terms (Manly et al. 2002). The resulting beta-coefficients (i.e., $\beta_1, \beta_2 \ldots \beta_n$) derived from the GLMM, or GLM for individual wolves, became the coefficients for the RSFs.

I used a ratio of 10:1 available points per used point. For all the data, I removed points occurring in water or rare habitat types (mixed swamp, sand dunes, white spruce). Rare habitat types accounted for <0.4% of the study area. I omitted points falling outside the Saskatchewan Boreal Shield Ecozone, as there exists no data for those areas. Prior to modelling, I scaled the continuous variables, elevation and distance to linear features, by centering them and dividing by two standard deviations using the function scale from the package arm (Gelman and Su 2018) in R statistical software. Variables were screened for collinearity using Pearson's correlation coefficients (Tabachnick et al. 2007). If two variables were collinear, I created two candidate models, each with one of the collinear terms dropped. I used habitat selection ratios to determine the reference category for each model. The reference category was the habitat class with the selection ratio closest to one, indicating neither strong selection nor avoidance (Manly et al. 2002).

For each season and scale, I fitted five potential candidate models: global, quadratic, interaction, simple, and habitat only (Table 3.2). I used Akaike's information criteria (AIC) to determine the model that best fits the data. I performed k-fold cross validation on the top models to determine predictive power of the model (Boyce et al. 2002). The data from each model was randomly split by individuals into five folds (Roberts et al. 2017). I estimated Spearman-rank correlations (R_S) between ten bins of RSF scores and area-adjusted frequencies. A strong, positive R_S is indicative of a model with good predictive capacity (Boyce et al. 2002). For the individual wolf RSFs I used similar methods as stated above only with the exception of the k-fold cross validation. The data were randomly split into five folds but each model considers only one individual so individual blocking was not used.

I preliminarily tested for a functional response to linear features by wolves where selection may change as a function of resource availability (Mysterud and Ims 1998). To do so, I assessed the strength of the correlation between the relative probability of selection and linear feature density when distance to linear features is zero meters and all other habitat variables are excluded.

3.2.7 Comparing habitat selection between species

To contrast the differences in habitat selection between wolves and boreal woodland caribou during the caribou calving and post-calving seasons, I employed latent selection difference (LSD). This method allows for direct comparison between two species or groups of interest. LSD uses the same equation as resource selection functions (equation 3.1), but $w(x)$ indicates the relative probability of one species (e.g. wolves; coded as 1) occurring on the landscape compared to another species (e.g. caribou; coded as 0). The selection coefficient (β_n) should be interpreted as relative difference in selection between wolves and caribou, not selection of a habitat unit as is with RSFs (Latham et al. 2011a). This model does not allow for individuals as random factors and therefore does not correct for unbalanced sampling design (Latham et al. 2011a).

I used LSDs to assess spatial separation between wolves and caribou. I used the same covariates that were used in the species RSF analyses, which included habitat class, elevation, and distance to linear features (see section *3.2.5 Environmental covariates*). I obtained caribou use-availability data from the calving and post-calving seasons from Superbie et al. (2019). The population study area for caribou was defined using 100% MCP around the individual home ranges (Figure 3.1). A key assumption is that all habitat types should be equally available to both species within the study area (Latham et al. 2011a). This assumption was not violated as I selected used points from the area of overlap of the species-in-question's respective study area (Figure 3.1). I truncated the use-availability data of wolves to match the beginning of the calving season and end of post-calving season (i.e. May 1 – Aug 11). I randomly selected one location per species per day during the calving and post-calving seasons. I used data from 2014 and 2015 in the wolf-caribou analysis.

I cleaned and prepared the data for the LSD using the same methods for the RSF analyses. I removed points occurring in water or rare habitat types (mixed swamp, sand dunes, white spruce). I omitted points falling outside the Saskatchewan Boreal Shield Ecozone, as there exists no data for those areas. Prior to modelling, I scaled the continuous variables, elevation and distance to linear features, by centering them and dividing by two standard deviations using the function scale from the package arm (Gelman and Su 2018) in R. I screened variables for collinearity using Pearson's correlation coefficients (Tabachnick et al. 2007). If two variables were collinear, I created two candidate models, each with one of the collinear terms dropped. I used habitat selection ratios to determine the reference category for each model. The reference

category was the habitat class with the relative selection ratio closest to one, indicating neutral relative difference in selection between species (Manly et al. 2002).

For each LSD, I fitted five potential candidate models: global, quadratic, interaction, simple, and habitat only (Table 3.2). I used AIC to determine the model that best fits the data. I calculated the relative operating characteristic curve (ROC) index to rate the probability that a model would correctly discriminate between one species and the other. ROC graphs plot the true positive rate, also called sensitivity, against the false positive rate, also called 1 - specificity (Swets 1988). The true positive rate is a measure of the proportion of sites at which the observations and predictions agree while the false positive rate is a measure of the proportion of disagreement between observations and predictions (Pearce and Ferrier 2000). Good model performance (i.e. high discrimination ability) is characterized by a curve that maximizes the true-positives while minimizing false-positives. Area under the curve (AUC) is calculated from the ROC where AUC values of 0.9 and above are indicative of high model accuracy, 0.7 to 0.9 good model accuracy, and less than 0.7 low model accuracy (Swets 1988).

3.2.8 Mapping habitat selection

To visualize the trends of the RSF and LSD analyses, I mapped the relative probabilities of selection of resource units (i.e., 30 × 30-m pixels) across the study area (Appendix E). I generated RSF maps for each season and scale for wolves and LSD maps for each species pair using raster layers of scaled elevation, scaled distance to linear features, and habitat classes (see section *3.2.5 Environmental covariates*). Continuous inputs were scaled using the formula:

$$(x - mean(x) \,/\, standard\ deviation(x)) \quad (3.4)$$

Maps were generated using the Raster Calculator function in ArcGIS Desktop, v. 10.5 (ESRI, 2018). The map formula was:

$$Exp((habitat\ raster) + [(\beta_8 * elevation\ raster) + (\beta_9 * elevation\ raster^2)] + [(\beta_{10} * distance\ to\ linear\ features\ raster) + (\beta_{11} * distance\ to\ linear\ features\ raster^2)] + (\beta_{12} * elevation\ raster * distance\ to\ linear\ features\ raster)) \quad (3.5)$$

where the habitat raster was altered to include the coefficients for each habitat class and the beta coefficients (β) for elevation and linear distance were entered manually for each season, scale,

and species combination. I rescaled the resulting raster so the predicted RSF values were between zero and one using the formula:

$(x - min(x))/(max(x) - min(x))$.....(3.6)

3.3 Results

3.3.1 Defining seasons for wolves

I defined seasons for the wolves using the range of peak points from the movement model (i.e., significant increases or decreases in the daily movement rate; Figure 3.3). The highest peaks occurred between May 11 and November 1. Those dates coincide with the approximate timing of snowmelt in spring and snow remaining on ground in fall estimated from weather stations in the study area. Combining the movement model with information on snowfall, I defined wolf seasons into snow-free (May 11 to October 31) and snow periods (November 1 to May 10).

3.3.2 Seasonal habitat selection by wolves

Over the period of 2014 – 2016, 37 wolves were collared. Of those 37 collars, 27 collars malfunctioned and went offline prematurely. Six of the 37 collars were dropped prematurely or otherwise stationary without mortality confirmation. Four of the 37 wolves were confirmed dead. Used points varied between seasons and scales. Used points averaged 18514 ± 7620 at the population scale and 16135 ±4447 at the home range scale (Table 3.3). Individual RSF analysis was possible for 13 wolves in both snow and snow-free seasons. The number of used points to each analysis averaged 1199 ± 550 points per individual across both seasons, with a minimum of 120 from one wolf in the snow season (Table 3.4). Only one collared individual per pack was used in each analysis.

Of the five candidate models estimated per season at the population scale, the global model had the lowest AIC value across both seasons (Table 3.5). The level of support for models was determined by the AIC values relative to the model with the lowest AIC. I selected the model with the lowest AIC but models within two ΔAIC represent models that are relatively equally supported and ΔAIC values greater than two have considerably less support (Burnham 2002). The global models included both quadratic and interaction terms for elevation and distance to linear features. The wolf home range analysis resulted in top models of quadratic and

global for the snow-free and snow seasons, respectively (Table 3.6). The top models for the individual wolf RSFs were all global or quadratic models (Table 3.7).

Wolf population scale models had intermediate predictive ability, mean R_S was 0.70 and 0.74 each in the snow-free and snow seasons, but average R_S across folds varied (Table 3.3). At the home range scale, wolf models predicted relatively poor, mean R_S was 0.54 and 0.39 in the snow-free and snow seasons, respectively (Table 3.3). Predictive ability of the individual wolf models was good, R_S ranged from 0.988 to 0.59 with the majority of individuals falling within 0.8 to 0.9 range (Table 3.4).

Across both snow and snow-free seasons at the population scale, wolves selected for open muskeg and avoided mature black spruce habitats. During the snow-free season, wolves relatively weakly avoided all other vegetation types. During the snow season, wolves relatively weakly selected for all other vegetation types except young-mid jack pine, for which wolves were selectively neutral (Table 3.8). In both the snow and snow-free seasons wolves were relatively selecting for lower elevations at the population scale. Wolves avoided linear features at the population scale but the trend appears to take a slight dip at intermediate distances (Figure 3.4).

At the home range scale, wolves selected for open muskeg and avoided mature black spruce in both seasons. In the snow-free season, wolves also selected for mature jack pine and young-mid black spruce while in the snow season, they selected for mixed coniferous-deciduous and young-mid jack pine (Table 3.9). In both seasons, wolves selected lower elevations at the home range scale (Figure 3.4). In the snow-free season wolves avoided linear features but also showed slightly higher relative probability of selection at low distances to linear features. In the snow season, wolves selected for linear features (Figure 3.4).

Individual wolves showed varied results in relative selection or avoidance of habitat classes, visual trends are not obvious (Appendix D, Table D.1a-c). Because wolves are social foragers and travel and hunt in pack units (Mech 1970), we can assume that habitat selection by the collared individual is representative of the pack. Consistent selection between packs for a habitat class only occurred with mixed coniferous-deciduous and open muskeg habitats during the snow season. Majority of packs selected for black spruce swamp, open muskeg, and young-mid black spruce and avoided young-mid jack pine in the snow-free season. Wolf packs generally selected for mixed coniferous-deciduous and open muskeg habitat and avoided young-

mid jack pine in the snow-season. Across both seasons, wolf individual pack response varied greatly to both elevation and linear features with no apparent general trend emerging among packs (Figures 3.5 and 3.6). I found a no functional response by wolves to linear features across varying linear feature densities ($R^2 = 0.07$, $p = 0.21$, Figure 3.7); however, I recommend caution when interpreting this result.

3.3.3 Comparing habitat selection between species

Within the range of overlap and one fix per species per day, analyses were run using $n = 1671$ points from 15 wolves and $n = 18939$ points from 83 caribou to compare wolves and caribou. Analyses comparing bears and wolves used $n = 598$ points from 15 bears and $n = 582$ from seven wolves (Table 3.10). Of the five candidate models estimated per species comparison, the global model had the lowest AIC value and thus the highest support across all three comparisons (Table 3.10). The global models included both quadratic and interaction terms for elevation and distance to linear features.

During the calving and post-calving seasons, wolves were less likely to use black spruce swamps, mature black spruce, and open muskegs and more likely to be found in mixed coniferous-deciduous and young coniferous stands compared to caribou. When comparing the two predators, bears were more likely to be found in mixed coniferous-deciduous and young-mid jack pine stands and less likely to be found in mature jack pine stands compared to wolves (Table 3.11). Wolves were slightly more likely to relatively select higher elevations compared to caribou. Wolves selected linear features relatively less than caribou and bears were less likely to be found at intermediate elevation compared to wolves over their combined range. Bears selected lower distances to linear features compared to wolves (Figure 3.8). I evaluated the latent selection difference models using ROC and AUC. The models performed well appearing to correctly discriminate between species. The wolf-caribou model was slightly less discriminatory than the bear-wolf model ($AUC_{wc} = 0.729$, $AUC_{bw} = 0.863$, Figure 3.9).

3.4 Discussion

3.4.1 Seasonal habitat selection by wolves

This study is the first of its kind to assess habitat selection for wolves in northern Saskatchewan. Past studies have focused on how wolves use human-dominated landscapes (Hebblewhite and

Merrill 2008, Houle et al. 2010, Latham et al. 2011b, Lesmerises et al. 2012, Dickie et al. 2017) while comparatively few have examined habitat selection by wolves in relatively natural systems (McLoughlin et al. 2004, Milakovic et al. 2011). While the general habits of wolves are well understood in more southern and northern ranges, little research has been done on wolves in the Boreal Shield of Saskatchewan, a unique region of boreal forest where anthropogenic impacts are minimal but fire disturbance is high. Wolves are habitat generalists, adapting habitat selection according to prey species availability (Mech and Boitani 2010), and as such, habitat selection varies across studies. In general, broad scale habitat selection patterns are reflective of limiting factors such as avoiding predation (Creel et al. 2005, McLoughlin et al. 2005, Dinkins et al. 2014), competition (Wereszczuk and Zalewski 2015, Duquette et al. 2017), and human mortality risk (Basille et al. 2013, Stillfried et al. 2015) and finer-scale habitat selection patterns reflect forage quality (Fortin et al. 2005, Boyce 2006). Generally, wolves select the habitat of their prey species that provide forage biomass or cover for ungulate prey (Houle et al. 2010, Courbin et al. 2014). Previous studies have found, in multi- prey systems, moose, elk, or deer to be primary prey of wolves and caribou are more likely to be opportunistic or alternative prey (Hebblewhite et al. 2003, Wittmer et al. 2005, Wittmer et al. 2007, Latham et al. 2011c). But in my study area, there are no elk or deer available and the moose are not likely the primary prey of wolves in my study area (McLoughlin et al. 2019, Neufeld et al. 2019)

Wolves in my study show variability in habitat selection between scales. At the population scale in the snow-free season, wolves avoid most habitats with the exception of open muskeg. The opposite is true in the winter, wolves select most habitats with the exception of avoiding mature black spruce. Avoidance of habitats likely indicates that such habitats do not provide the quality necessary to sustain wolf populations (Bjørneraas et al. 2012, Uboni 2012, Grilo et al. 2019). Wet habitats such as black spruce swamp, in the snow-free season, could present barriers to efficient movement or be too wet to provide enough habitable area. Selection of more wet habitat types in winter could relate to ability to travel as many wet areas or open waters no longer provide barriers to movement (Kuzyk et al. 2004, Johnson et al. 2017) At the population scale during the snow-free season, wolves avoided young conifer habitat, likely because coarse woody debris in large tracts of young burns could present barriers to efficient travel (Brais et al. 2005). Wolves continued to avoid young-mid jack pine stands at the home range scale in winter. But during the snow-free season, at the home range scale, wolves selected

for young black spruce habitats. Collectively, young and mid-aged coniferous stands account for almost all of the recently burned habitat in the Saskatchewan Boreal Shield and 42.2% of the land base (McLoughlin et al. 2019). While these are early-seral habitats, they are resilient towards fire and often return as coniferous stands even after short-interval fires (Hart et al. 2019). These habitats do not provide adequate browse for moose, lacking substantial willow (*Salix* spp.), trembling aspen (*Populus tremuloides*), birches (*Betula* spp.), and green alder (*Alnus viridis*; Shipley 2010, Neufeld et al. 2019). Moose may not have the same opportunities to respond to disturbance in the Boreal Shield of Saskatchewan as in the more southern and western range of boreal caribou. That wolves generally avoid these habitats of <40 years of age, suggests that these vegetation associations are not supporting alternate prey like moose, or if they are, wolves are not strongly seeking them out. Instead, ideal moose habitat (the only other ungulate prey source for wolves) in my study area likely lies within the mixed-coniferous habitats (Neufeld et al. 2019), for which wolves select in the winter at both scales.

Interestingly, across all seasons and scales, wolves avoided mature black spruce and selected for open muskeg habitats. Caribou in the study area generally select for mature black spruce stands (Superbie et al. 2019) but apparently are not a draw for wolves in that habitat type. Mature black spruce could therefore represent a refuge for caribou in my study area (Rettie and Messier 2000, Superbie et al. 2019). Although other habitats exist where wolves and caribou could be interacting, such as open muskegs, for which caribou generally select across seasons (Superbie et al. 2019). Some studies regarding caribou consider selection of wetlands to provide refuge from predators (James et al. 2004, Latham et al. 2011a), but open muskegs may also provide preferable moose forage (Timmermann and McNicol 1988, Shipley 2010), which could draw in wolves.

Beaver can be an important component of wolf diet (Latham et al. 2013, Moayeri 2013, Gable et al. 2016, Found et al. 2018, Gable et al. 2018), including in Saskatchewan (Urton and Hobson 2005). Across the Boreal Shield of Saskatchewan, there exists a vast network of waterways that likely provide habitat for beavers. Beavers select habitat based on a variety of characteristics including stream gradient, stream size and depth, watershed size, valley or floodplain width, substrate type, and riparian slope (Touihri et al. 2018). Wolves in my study area select for lower elevations at both scales and seasons, likely linked with drainages (i.e. potential beaver habitat) across the landscape. But as beavers are largely unavailable in the

winter as they remain below the ice (Smith and Peterson 1991), perhaps use of natural linear features such as frozen rivers or streams within low elevation drainages is driving wolf selection in the snow season (Droghini and Boutin 2017, Johnson et al. 2017).

Beavers are central place foragers consuming a variety of graminoids, herbaceous and aquatic plants, shrubs, and trees with decreasing effort with distance from edge of water (McGinley and Whitham 1985). Deciduous tree cover is often an important variable positively related to beaver habitat selection (Slough and Sadleir 1977, Boyce 1981, Dieter and McCabe 1989, Cotton 1990, McComb et al. 1990, Curtis and Jensen 2004). Although I cannot comment on the effects of waterway variables in my study area, from the habitat perspective, it is possible that beavers would select habitat in or near mixed coniferous-deciduous stands as they are the only category providing adequate deciduous cover. The Ecosite classes within open muskeg habitat (see Stewart 2016), while wet, often presents as a matrix of water, soil, and vegetation rather than open water (Figure 3.2). In addition, deciduous trees are not found in open muskeg habitats (McLaughlan et al. 2010), therefore it is unlikely that beavers are driving wolf selection of open muskeg habitat. However, beavers are still able to occupy areas where preferred deciduous species are absent and are capable of surviving in coniferous areas (Brenner 1962, Jenkins 1975). Populations of beavers are known to exist and be consumed by wolves in northern habitats (Urton and Hobson 2005, Moayeri 2013) but perhaps my habitat classes designed for large mammals and ignoring waterways, are not applicable nor fine enough to relate to beaver.

Wolf responses to linear features were evident only over relatively large distances. Effect sizes on probability of selection over smaller ranges (e.g. 1000 m) was not detectable; but over larger distances I found wolves to be farther from linear features during both seasons at the population scale and during the snow-free seasons at the home range scale. Wolves relatively selected for linear features in the snow season at the home range scale. Wolves often use linear features to travel efficiently across the landscape (Dickie et al. 2017). But in winter, buildup of snow on open linear features can lead to a decrease in travel speed and subsequent use (Latham et al. 2011b, Dickie et al. 2017). In some cases, linear features with snow that has been compacted can still serve as effective travel corridors (Droghini and Boutin 2017). Wolf habitat selection is often driven strongly by human disturbance in population ranges where human activity is prominent (Hebblewhite and Merrill 2008, Lesmerises et al. 2012). A habitat functional response, which describes a change in selection of a habitat feature with a change in

that feature's availability (Mysterud and Ims 1998), has been shown for wolves in regards to anthropogenic landscape features (Hebblewhite and Merrill 2008, Dickie et al. 2017, DeMars and Boutin 2018).

Wolves are expected to use linear features where advantages are gained in terms of increasing encounter rates with prey. While wolf encounter rates can be a positive function of linear density (McKenzie et al. 2012), in the Saskatchewan Boreal Shield line density across the study area landscape averaged 0.14 km/km^2, more than an order of magnitude lower than observed in other wolf ranges (Latham et al. 2011b, DeMars and Boutin 2018). Simultaneously, ungulate density is much lower compared to other wolf ranges (Neufeld et al. 2019). In the wolf predator-prey encounter rate models of McKenzie et al. (2012), the combination of low prey density and low linear feature density resulted in the lowest expected encounter rates of prey by wolves. Caribou response to linear features in my study area is highly scale-dependent with caribou generally selecting linear features at the population scale but avoiding them at the home range scale (Superbie et al. 2019). Without consistent prey attraction to linear features, it would not be advantageous for wolves to bias their movements towards linear features at low feature density (McKenzie et al. 2012).

Conversely, avoidance of linear features can occur as a product of the associated human activity on linear features, which wolves are known to avoid (Whittington et al. 2005, Rogala et al. 2011). The benefits of linear features for travel could be outweighed by encounters with humans when linear features become more abundant (Whittington et al. 2005). Broadly, human activity in my study area is low and it is not comparable to the levels of human activity where these functional responses were found (McLoughlin et al. 2019, Latham et al. 2011, DeMars and Boutin 2018), therefore it is unlikely to be advantageous for wolves to bias movements away from linear features as well. However, there exists no indication of human activity on different line types in my study area. Line types in my study area include major gravel highways, electrical utility corridors, fire breaks, survey cutlines, minor roads, and trails which vary greatly in human use. As a result, it is difficult to confidently associate wolf selection patterns to human activity as human activity can also vary over line types. I posit that wolves may not respond to linear feature density at low feature densities found in my study area; however, the evidence of a functional response should be interpreted with extreme caution. This analysis is limited by calculating wolf response only at a short distance to linear features and excluding all other model

variables and therefore ignores wolf response across the entire breadth of availability and habitat. Further analysis is necessary to fully understand wolf response to linear features in a low line density environment.

Wolf packs in the Saskatchewan Boreal Shield vary greatly in habitat selection patterns. Given that wolves are obligate carnivores and social foragers, I expected wolves of a population would not diverge greatly in their habitat selection patterns; however, a diet study of wolves in Saskatchewan also found greater than expected variation among individuals (Urton and Hobson 2005). For generalist species, patterns of habitat selection at the population scale can often mask important patterns for individuals or packs (Latham et al. 2011a, Lesmerises and St-Laurent 2017). Generalist species have an ability to use a wide range of food sources and habitats allows them to exhibit behavioural plasticity in response to varying resources across the landscape (Lesmerises and St-Laurent 2017). With the low densities of ungulate prey in the Saskatchewan Boreal Shield, they cannot rely on a single prey species to fulfill energetic needs. Partial variation in pack response could be explained by differences in home range location across the landscape and what is available in terms of habitat and prey density. In both seasons, all habitat classes had varying trends regarding wolf pack selection for habitat types with the exception of consistent selection for mixed coniferous-deciduous and open muskeg habitats by individuals in the snow season, which matches the population and home range scale results. Interestingly, caribou selection for mature conifer stands and treed bogs may not provide the suspected refuge from some wolf packs. In addition, young-mid coniferous stands are not equal to wolves. Packs generally select for young black spruce stands and avoid young jack pine stands. It is unclear what the difference is between these two stand types that is driving wolf selection but the opposite trend is seen with a few packs as well. Wolf variation is perhaps best visualized in regards to elevation and distance to linear features where it is impossible to define a consistent trend across packs. Lack of a strong response to linear features is still evident at the individual pack level, responses to linear features vary in direction.

Predictive ability of the individual pack models was much greater than that of the population and home range models. While population level trends were moderately captured by the models, the variability in wolf habitat selection at the home range scale was reflected by the poor predictability. Individual pack level models, however, were highly predictive indicating that while wolf diet was variable between packs, it remained consistent within packs. It makes sense,

given the generalist nature of wolves, that predictive ability of the larger-scale models might be weak. It was somewhat unexpected to see such variability not reflected in the individual pack models. The variability in habitat selection between packs but consistency within packs leads me to suspect that packs are specializing on specific prey species. Pack size is reflective of the primary prey base used by wolves as prey size influences hunting tactics and risk to wolves (Barber-Meyer et al. 2016). Average pack size in my study area is 4.0 wolves/pack ranging from 2-10 wolves in a pack (Neufeld et al. 2019). The range of sizes indicate that packs are numerically equipped to hunt a range of prey sizes. There were wolves collared in my study area that were suspected to make seasonal movements with the migratory barren-ground caribou (Neufeld et al. 2019), although they are not included in my analyses. A diet study on wolves in the Boreal Plains Ecozone of Saskatchewan identified elk as primary prey, followed by whitetail, moose, beaver, and snowshoe hare (Urton and Hobson 2005). The same prey base is not available to wolves in the Boreal Shield Ecozone; ideally, a diet study would confirm the diet of wolves in my study area.

3.4.2 Comparing habitat selection between species

In Chapter 2, I found that habitat overlap between bears and caribou was minimal during the calving and post-calving seasons. Caribou in my study area select for black spruce (*Picea mariana*) bogs and open muskegs during the calving and post-calving seasons (Superbie et al. 2019). Wolves were significantly less likely to be found in caribou calving habitats although to a smaller effect size than that of bears and caribou. Wolves and caribou differ little in selection for elevation. Interestingly, wolves are found a greater distances to linear features compared to caribou. But in the case of each species, neither is found relatively close to linear features (Superbie et al. 2019). Both predators maintained spatial separation across most habitat types and the model was able to correctly discriminate between bears and wolves. Notably, the wolf-caribou model was the least discriminatory compared to the predator comparison and the bear-caribou comparison (see Chapter 2). The results suggest that wolves and caribou differed less in their patterns of resource selection during the calving and post-calving season than did bears and caribou or bears and wolves. Caribou are likely maintaining adequate spatial separation from wolves during times of peak calf-vulnerability but calves are more at risk from predation by wolves than by black bears in my study area. In the discussion of predator-prey relationships, the focus remains on black bears as important potential predators of juvenile ungulates. We must not

disregard wolves as the ultimate predator of caribou, juveniles included, in certain landscapes such as the Boreal Shield of Saskatchewan.

The calving and post-calving seasons (calving: May 1 – June 15, post-calving: June 16 – August 11) span the black bear hunting season in the study area (April 15 – June 30). During the hunting season, active baits exist throughout the study area. While these baits are not targeting wolves, they have been known to use them on occasion, specifically if they are baited with meat or fish waste (P.D. McLoughlin, University of Saskatchewan, pers. obs.). Consistent feeding at bait stations could alter habitat selection during that time. Similar baiting techniques have been assessed as potential diversionary feeding sites to draw wolves away from ungulate neonates during calving seasons (Boertje et al. 2010), and from livestock (Rossler et al. 2012). Bear baits during the hunting season could act similarly, drawing wolves away from ungulate neonates to a more reliable, easily accessed food source. This depends on the baits being supplied with meat over other baiting options that only appeal to bears. Wolves also are unable to access bait barrels as easily as bears and therefore cannot exploit the bait as freely.

3.4.3 Conclusions

This study was the first to assess habitat selection patterns of wolves in the Boreal Shield of Saskatchewan. While wolf selection patterns are relatively well-studied in areas of high anthropogenic disturbance, my study was the first to consider such patterns at the low levels of anthropogenic disturbance as seen in my study area. I found a no significant functional response to linear features in my study area; however, analyses are preliminary and would benefit from further exploration. The variation of linear features across pack home ranges is notable and merits further exploration with additional information on linear feature types. Scale of assessment plays an important role in the outcomes of a habitat selection. Many studies have concluded the importance of scale in management decisions and my study area is no different.

My results suggest the wolves have variable habitat selection patterns at the population and home range scales but are highly predictable as pack units. My data generally support the proposal by Neufeld et al. (In prep) that caribou are likely the most important prey item for wolves in the Boreal Shield of Saskatchewan. Consistent, predictable habitat selection for individual packs suggest the potential for pack specialization for specific prey. Wolves in my study area likely prey on caribou, moose, or beaver for the majority of their diet but a diet analysis is needed to confirm these predictions.

Wolves have greater habitat overlap with caribou than they do with bears or bears with caribou. My results suggest that wolves do not spend the majority of their time in caribou habitat, specifically during the calving and post-calving seasons; hence, caribou are somewhat successfully spatially separating from predators during a time of greatest calf vulnerability. Between bears and wolves, my data suggest that the latter are a more important predator to caribou.

3.5 Tables and Figures

Table 3.1. Descriptions for the seven habitat classes used to characterize resource units (30 × 30-m pixels of land) in the Boreal Shield of Saskatchewan. Percent (%) area represents the percentage of land surface area (excluding water) covered by each habitat class within the Boreal Shield of Saskatchewan at the beginning of our study (May 2016). Canopy cover refers to the area of the ground in a site shaded by the canopy species. Note that the 0.38% of area unaccounted for is attributed to rare habitat classes not included in the models. Table adapted from Superbie et al. (2019).

Habitat class	% Area	Description
Mature jack pine	21.02	Canopy dominated by jack pine (*Pinus banksiana*) trees > 40 years old. Black spruce (*Picea mariana*) commonly co-occurs in small amounts (total canopy cover est. <15%).
Young-mid jack pine forest	36.54	Jack pine-dominated forests ≤ 40 years post-fire. These sites are expected to support fewer terrestrial lichens than sites dominated by mature jack pine forest.
Mature black spruce	8.38	Canopy dominated by black spruce forest > 40 years old. Terrestrial lichens comprise > 40% of the ground cover in some sites.
Young-mid black spruce forest	5.59	Black spruce-dominated forests ≤40 years post-fire. These sites are expected to support fewer terrestrial lichens than sites dominated by mature black spruce forest.
Mixed coniferous-deciduous	7.33	Either mixed deciduous forest comprised of trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) or mixed coniferous-deciduous forest comprised of black spruce trembling aspen and/or white birch. The overstory tends to be dense relative to the other habitat classes (total canopy cover est. > 48%).
Black spruce swamp	11.43	Somewhat open, black spruce-dominated canopy, generally comprised of mature trees (i.e., trees > 40-years old). Understory dominated by ericaceous shrubs. Terrestrial lichens comprise ~16% of ground cover.
Open muskeg	9.33	Lowland bog or fen habitats with generally low tree and shrub cover; some sites may support stands of tamarack trees (*Larix laricina*) or a dense clusters of shrubs, especially willow (*Salix* sp.) and river alder (*Alnus* sp.).

Table 3.2. Variables included in each of five mixed-effect logistic regression models used to assess habitat selection for wolves and compare habitat selection between wolves, black bears, and boreal woodland caribou in the Boreal Shield of Saskatchewan.

Model	Variables
Global	Habitat + Elevation² × LinDist²
Quadratic	Habitat + Elevation² + LinDist²
Interaction	Habitat + Elevation × LinDist
Simple	Habitat + Elevation + LinDist
Habitat only	Habitat

Table 3.3. Sample size of GPS fixes (*n*) and number of individuals (*N*) used to develop generalized linear mixed models estimating seasonal resource selection at two scales for populations of wolves in the Boreal Shield of Saskatchewan and associated Spearman-rank correlation between ten Resource Selection Function (RSF) bins and area-adjusted frequencies for individually blocked five-fold (F1, F2, F3, F4, F5) cross validation. Mean represents the average Spearman-rank correlation of the five folds.

Scale	Season	*n*	*N*	Spearman- rank correlation					
Population	Snow-free	23902	18	0.552	0.733	1.000	0.964	0.255	0.701
	Snow	13126	14	0.927	0.830	0.770	0.709	0.455	0.738
Home range	Snow-free	19279	13	0.830	0.358	0.636	0.709	0.212	0.549
	Snow	12990	13	0.891	0.358	0.370	-0.224	0.576	0.394

Table 3.4. Sample size of GPS fixes (*n*) used to develop generalized linear mixed models estimating seasonal resource selection of individual wolves in the Boreal Shield of Saskatchewan and associated Spearman-rank correlation between ten Resource Selection Function (RSF) bins and area-adjusted frequencies for individually blocked five-fold (F1, F2, F3, F4, F5) cross validation. Mean represents the average Spearman-rank correlation of the five folds.

			Spearman- rank correlation					
Season	Wolf ID	*n*	F1	F2	F3	F4	F5	Mean
Snow-free	140004	2399	0.988	0.988	1.000	0.979	0.988	0.988
	140005	2299	0.927	0.952	0.976	0.927	0.976	0.952
	140007	1200	0.964	0.973	0.976	0.794	0.939	0.929
	140008	1716	0.976	0.976	0.912	0.915	0.942	0.944
	140010	2340	0.964	0.976	0.952	0.939	0.952	0.956
	140017	1142	0.976	0.839	0.952	0.915	0.954	0.927
	140019	1181	0.697	0.612	0.827	0.915	0.867	0.784
	140021	989	0.976	0.988	0.969	0.988	0.985	0.981
	140027	1209	0.915	0.939	0.976	0.976	0.879	0.937
	140030	1218	0.842	0.802	0.863	0.927	0.782	0.843
	140037	1125	0.936	0.915	0.891	0.964	0.891	0.919
	140038	1242	0.952	0.942	0.960	0.960	0.939	0.951
	140039	1219	0.976	0.973	0.985	0.985	0.982	0.980
Snow	140004	1417	0.936	0.988	0.948	0.976	0.912	0.952
	140005	1266	0.879	0.879	0.939	0.754	0.721	0.834
	140007	1344	0.891	0.891	0.821	0.867	0.842	0.862
	140008	1404	0.964	0.960	0.976	0.973	0.954	0.965
	140010	1340	0.964	0.973	0.952	0.985	0.976	0.970
	140017	986	0.952	0.976	0.857	0.879	0.988	0.930
	140019	937	0.912	0.906	0.818	0.957	0.906	0.900
	140021	740	0.979	0.891	0.903	0.964	0.868	0.921
	140027	833	0.903	0.952	0.964	0.784	0.863	0.893
	140030	253	0.770	0.591	0.505	0.509	0.576	0.590
	140037	649	0.830	0.952	0.924	0.894	0.918	0.903
	140038	612	0.830	0.796	0.872	0.742	0.976	0.843
	140039	120	0.939	0.903	0.855	0.964	0.806	0.893

Table 3.5. Comparison of models used to predict resource selection at the population scale for wolves in the Boreal Shield of Saskatchewan. Models are ranked based on Akaike's information criteria (AIC) values. Delta AIC (ΔAIC) measures the difference between each model and the top model and Akaike weights (w_i) indicates the probability that a model is best among an entire set of candidate models.

Season	Model	AIC	ΔAIC	w_i
Snow-free	Habitat + Elev² × LinDist²	151564.4	0	1
	Habitat + Elev² + LinDist²	151669.8	105.4	<0.001
	Habitat + Elev × LinDist	152698.5	1134.1	<0.001
	Habitat + Elev + LinDist	152698.9	1134.5	<0.001
Snow	Habitat + Elev² × LinDist²	83326.5	0	0.947
	Habitat + Elev² + LinDist²	83332.2	5.7	0.053
	Habitat + Elev × LinDist	83403.4	77	<0.001
	Habitat + Elev + LinDist	83410.6	84.1	<0.001

Table 3.6. Comparison of models used to predict resource selection at the home range scale for populations of wolves in the Boreal Shield of Saskatchewan. Models are ranked based on Akaike's information criteria (AIC) values. Delta AIC (ΔAIC) measures the difference between each model and the top model and Akaike weights (w_i) indicates the probability that a model is best among an entire set of candidate models.

Season	Model	AIC	ΔAIC	w_i
Snow-free	Habitat + Elev² + LinDist²	125038.5	0	0.71
	Habitat + Elev² × LinDist²	125040.3	1.8	0.29
	Habitat + Elev × LinDist	125214.3	175.8	<0.001
	Habitat + Elev + LinDist	125258.1	219.6	<0.001
	Habitat	128736.6	3698.1	<0.001
Snow	Habitat + Elev² × LinDist²	84971.2	0	1
	Habitat + Elev × LinDist	85100.2	129	<0.001
	Habitat + Elev² + LinDist²	85328.5	357.3	<0.001
	Habitat + Elev + LinDist	85329.6	358.4	<0.001
	Habitat	86184.2	1213	<0.001

Table 3.7. Summary of Akaike's information criteria (AIC) values and Akaike weights (w_i) of top models used to predict resource selection by individual wolves in the Boreal Shield of Saskatchewan. Akaike weights (w_i) indicates the probability that a model is best among an entire set of candidate models. Full dataset including other candidate models can be found in Appendix C.

Season	Wolf	Model	AIC	w_i
Snow-free	140004	Habitat + Elevation² + LinDist²	13541.6	0.68
	140005	Habitat + Elevation² × LinDist²	14872.8	1
	140007	Habitat + Elevation² + LinDist²	7596.7	0.72
	140008	Habitat + Elevation² × LinDist²	11023	0.79
	140010	Habitat + Elevation² + LinDist²	14386.9	0.572
	140017	Habitat + Elevation² × LinDist²	6886.9	0.987
	140019	Habitat + Elevation² × LinDist²	7673.2	0.83
	140021	Habitat + Elevation² × LinDist²	4577.4	1
	140027	Habitat + Elevation² × LinDist²	7705.6	1
	140030	Habitat + Elevation² × LinDist²	7142.7	1
	140037	Habitat + Elevation² × LinDist²	6719.5	1
	140038	Habitat + Elevation² × LinDist²	7386.6	0.9965
	140039	Habitat + Elevation² × LinDist²	7019.3	1
Snow	140004	Habitat + Elevation² + LinDist²	8671.9	0.73
	140005	Habitat + Elevation² × LinDist²	8107.8	1
	140007	Habitat + Elevation² × LinDist²	7449	1
	140008	Habitat + Elevation² × LinDist²	7398.2	1
	140010	Habitat + Elevation² + LinDist²	7590.4	0.54
	140017	Habitat + Elevation² × LinDist²	5945.8	1
	140019	Habitat + Elevation² × LinDist²	6018.5	0.71
	140021	Habitat + Elevation² + LinDist²	4460.7	0.71
	140027	Habitat + Elevation² × LinDist²	5286.6	0.936
	140030	Habitat + Elevation² + LinDist²	1634.1	0.343
	140037	Habitat + Elevation² × LinDist²	4065.8	0.997
	140038	Habitat + Elevation² × LinDist²	3842.6	1
	140039	Habitat + Elevation² × LinDist²	7776.9	0.936

Table 3.8. Summary of beta coefficients (β) ± standard error (SE), and *p*-values (*P*) for generalized linear mixed models predicting seasonal resource selection at the population scale for a gray wolf population in the Boreal Shield of Saskatchewan.

	Snow-free				Snow			
Variable	β	SE	*P*		β	SE	*P*	
Black Spruce Swamp	-0.080	0.024	0.001	*	0.193	0.043	<0.001	*
Mature Black Spruce	-0.789	0.029	<0.001	*	-0.358	0.046	<0.001	*
Mature Jack Pine	-2.461[a]	0.029	<0.001	*	0.110	0.042	0.010	*
Mixed Con-Dec	-0.295	0.028	<0.001	*	0.274	0.043	<0.001	*
Open Muskeg	0.141	0.024	<0.001	*	0.674	0.041	<0.001	*
Young-Mid Black Spruce	-0.183	0.029	<0.001	*	-2.545[a]	0.077	<0.001	*
Young-Mid Jack Pine	-0.230	0.021	<0.001	*	0.034	0.041	0.405	
Elevation	-0.638	0.009	<0.001	*	-0.688	0.013	<0.001	*
Elevation^2	0.023	0.008	0.002	*	-0.070	0.011	<0.001	*
LinDist	-0.190	0.010	<0.001	*	-0.062	0.013	<0.001	*
LinDist^2	0.174	0.005	<0.001	*	0.052	0.008	<0.001	*
Elevation x LinDist	-0.070	0.007	<0.001	*	0.030	0.011	0.006	*

[a] Indicates reference habitat class for that season
* Indicates P≤0.05

Table 3.9. Summary of beta coefficients (β) ± standard error (SE), and *p*-values (*P*) for generalized linear mixed models predicting seasonal resource selection at the home range scale for a gray wolf population in the Boreal Shield of Saskatchewan.

	Snow-free				Snow			
Variable	β	SE	*P*		β	SE	*P*	
Black Spruce Swamp	0.038	0.034	0.262		0.029	0.035	0.400	
Mature Black Spruce	-0.422	0.039	<0.001	*	-0.207	0.040	0.000	*
Mature Jack Pine	0.126	0.033	0.000	*	-2.070 [a]	0.256	0.000	*
Mixed Con-Dec	-2.310 [a]	0.303	0.000	*	0.492	0.036	<0.001	*
Open Muskeg	0.163	0.034	0.000	*	0.432	0.033	<0.001	*
Young-Mid Black Spruce	0.132	0.037	0.000	*	-0.083	0.042	0.050	
Young-Mid Jack Pine	-0.055	0.032	0.086		-0.194	0.031	0.000	*
Elevation	-1.196	0.022	<0.001	*	-0.762	0.025	<0.001	*
Elevation²	-0.036	0.012	0.002	*	-0.058	0.013	0.000	*
LinDist	-0.226	0.013	<0.001	*	-0.012	0.015	0.444	
LinDist²	0.084	0.006	<0.001	*	-0.089	0.008	<0.001	*
Elevation x LinDist	NA	NA	NA		0.233	0.013	<0.001	*

[a] Indicates reference habitat class for that season
* Indicates P≤0.05

Table 3.10. Comparison of latent selection difference (LSD) models used to compare resource selection during the calving and post-calving seasons between wolves and boreal woodland caribou and black bears and wolves in the Boreal Shield of Saskatchewan. Models were run using *n* fixes from each species of *N* individuals. Models are ranked based on Akaike's information criteria (AIC) values. Delta AIC (ΔAIC) measures the difference between each model and the top model and Akaike weights (w_i) indicates the probability that a model is best among an entire set of candidate models.

Species	*n*	*N*	Model	AIC	ΔAIC	df	w_i
Wolf	1671	15	Habitat + Elev² × LinDist²	10876.7	0	12	0.79
			Habitat + Elev² + LinDist²	10879.3	2.6	11	0.21
Caribou	18939	83	Habitat + Elev × LinDist	11023	146.3	10	<0.001
			Habitat + Elev + LinDist	11032.4	155.7	9	<0.001
			Habitat	11240.3	363.6	8	<0.001
Bear	598	15	Habitat + Elev² + LinDist²	1083.5	0	11	0.67
			Habitat + Elev² × LinDist²	1085	1.5	12	0.33
Wolf	582	7	Habitat + Elev + LinDist	1113	29.5	9	<0.001
			Habitat + Elev × LinDist	1113.1	29.5	10	<0.001
			Habitat	1620.2	536.7	7	<0.001

Table 3.11. Summary of beta coefficients (β) ± standard error (SE), and *p*-values (*P*) for latent selection difference (LSD) models comparing resource selection during the calving and post-calving seasons for wolves and boreal woodland caribou and black bears and wolves in the Boreal Shield of Saskatchewan.

	WolfCaribou				BearWolf			
Variable	β	SE	*P*		β	SE	*P*	
Black Spruce Swamp	-0.521	0.086	<0.001	*	-0.241	0.243	0.321	
Mature Black Spruce	-0.442	0.114	<0.001	*	-0.082	0.317	0.796	
Mature Jack Pine	-2.692	0.069	<0.001	*	-1.126	0.253	<0.001	*
Mixed Con-Dec	1.560	0.125	<0.001	*	0.688	0.309	0.026	*
Open Muskeg	-0.202	0.085	0.018	*	-0.310	0.275	0.258	
Young-Mid Black Spruce	0.258	0.112	0.022	*	0.423	0.333	0.204	
Young-Mid Jack Pine	0.170	0.078	0.030	*	0.898	0.305	0.003	*
Elevation	-0.513	0.031	<0.001	*	0.277	0.085	0.001	*
Elevation²	0.007	0.031	0.813		0.261	0.073	<0.001	*
LinDist	-0.159	0.039	<0.001	*	-2.580	0.232	<0.001	*
LinDist²	0.208	0.017	<0.001	*	-1.216	0.365	<0.001	*
Elevation x LinDist	0.043	0.020	0.032	*	NA	NA	NA	

[a] Indicates reference habitat class for that season
* Indicates P≤0.05

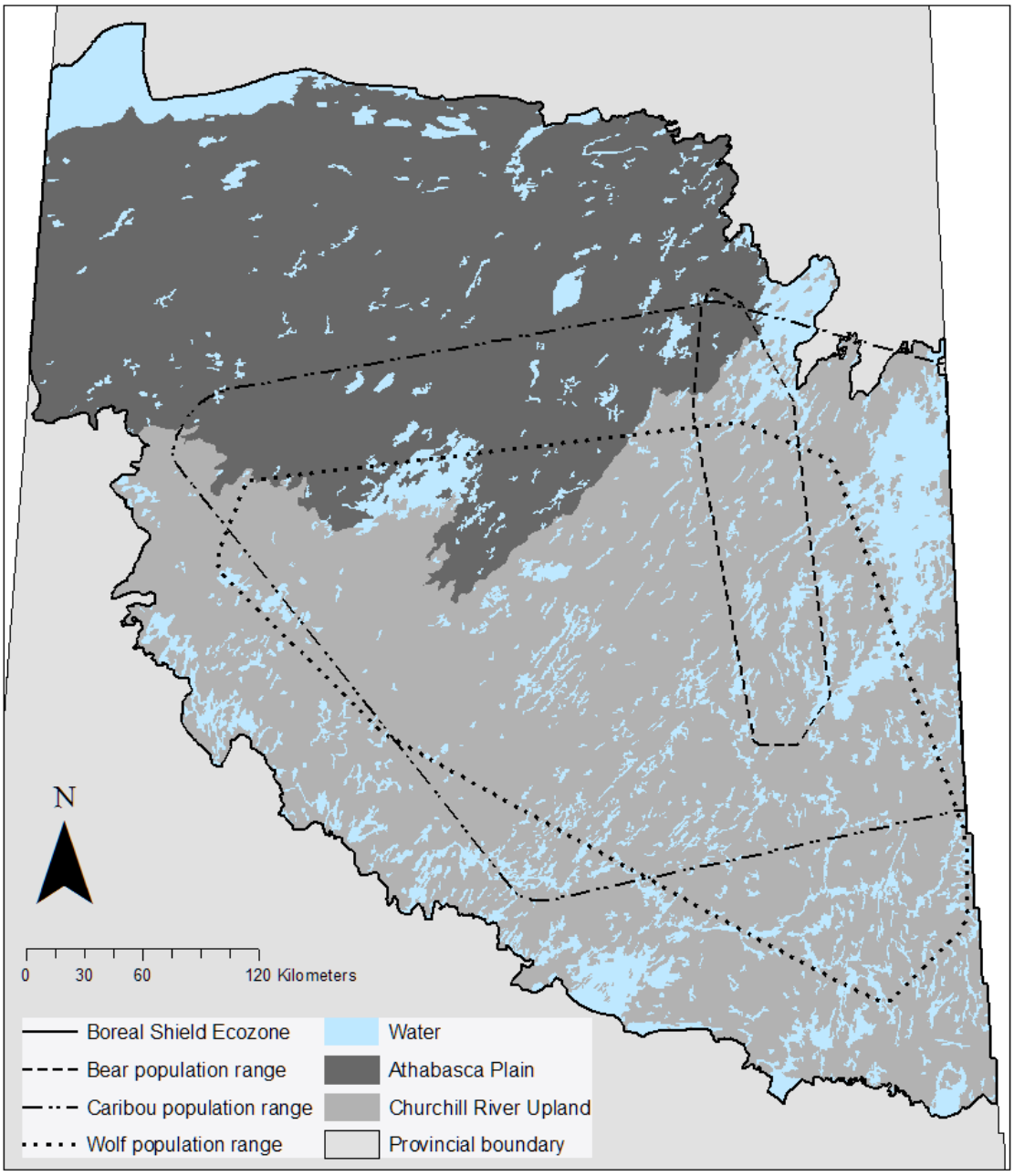

Figure 3.1. Location of the study area for black bears, gray wolves, and boreal woodland caribou within the Boreal Shield of Saskatchewan. The study area differed slightly for each species, indicated by the dashed and dotted lines. The study area for black bears and wolves was defined as the 100% minimum convex polygon (MCP) around all GPS fixes for each species, excluding dispersers. The study area for caribou is defined as the population range of boreal caribou with sufficient data to compute kernel-density home ranges.

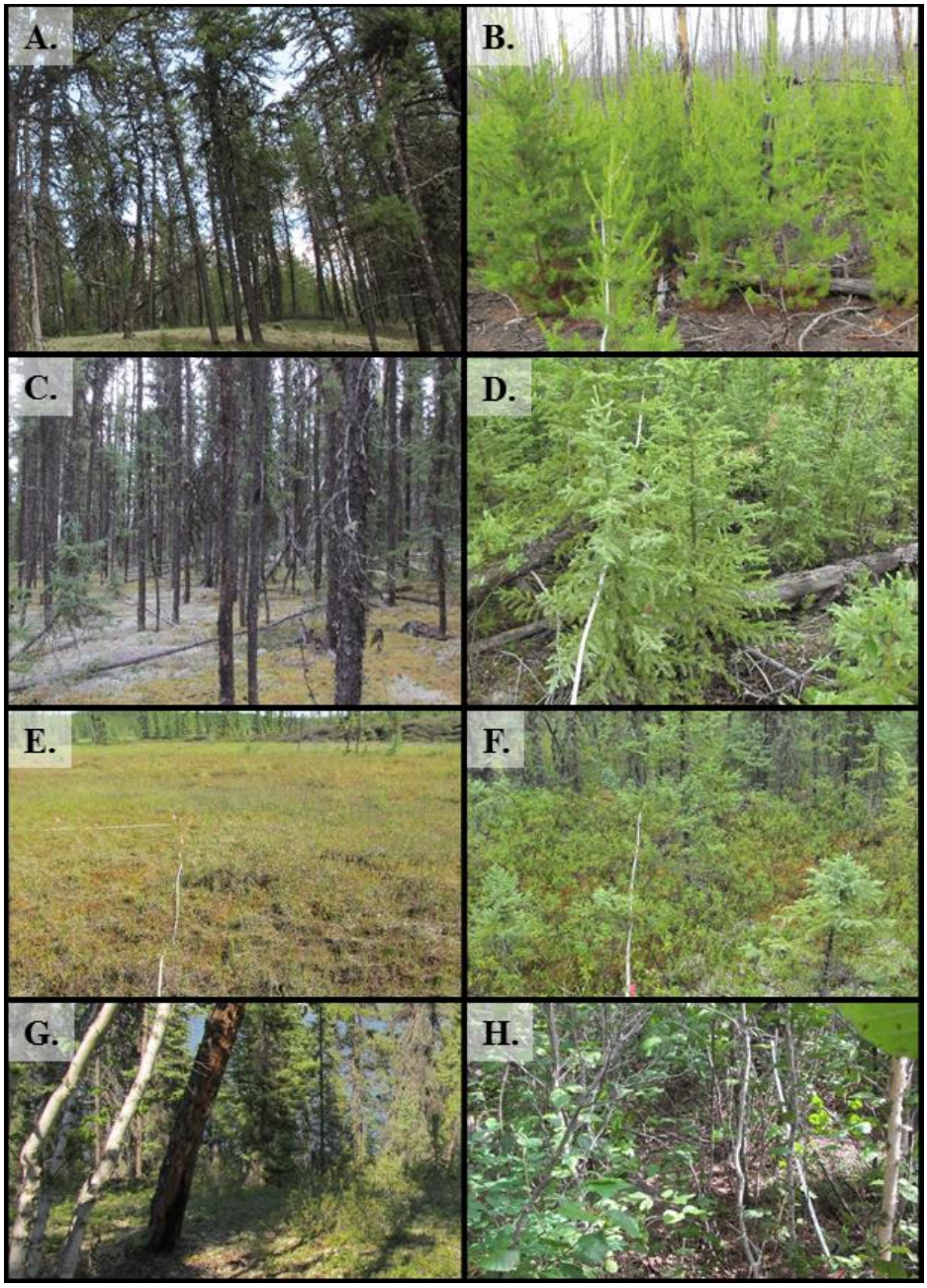

Figure 3.2. Images of the seven habitat classes used to characterize the environment and model resource selection by wolves in the Boreal Shield of Saskatchewan. A. Mature (> 40 years) jack pine forest; B. Early successional (≤ 40 years) jack pine forest; C. Mature black spruce forest; D. Early successional black spruce forests; E. Open muskeg; F. Black spruce swamp; F. Mixed coniferous-deciduous forests; H. Early successional deciduous forests. Habitat G and H were pooled for analysis. Photo credit: Ruth Greuel. Figure adapted from McLoughlin et al. 2019.

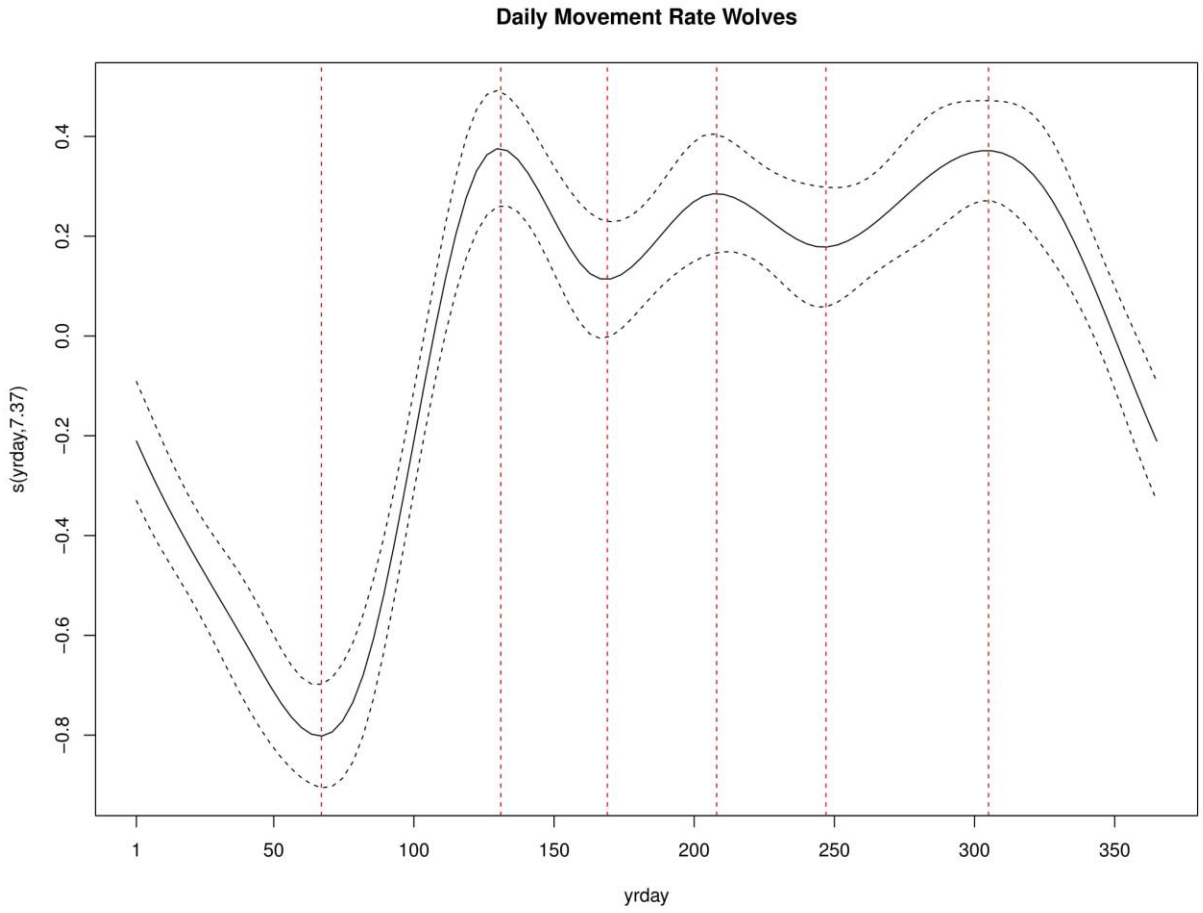

Figure 3.3. A generalized additive mixed model fitted to the log daily movement rate (m/h/day) of nine wolves (s(yrday, 7.37)) as a smoothed function of Julian date (yrday). The solid line is the predicted daily movement rate and the dashed lines alongside represent confidence intervals (2× the standard error of prediction). The units on the y-axis have been scaled to linear units so that the predicted values are centered on zero. Seasonal boundaries (vertical dashed lines) were delineated using local maxima and minima (i.e., significant increases or decreases in the daily movement rate).

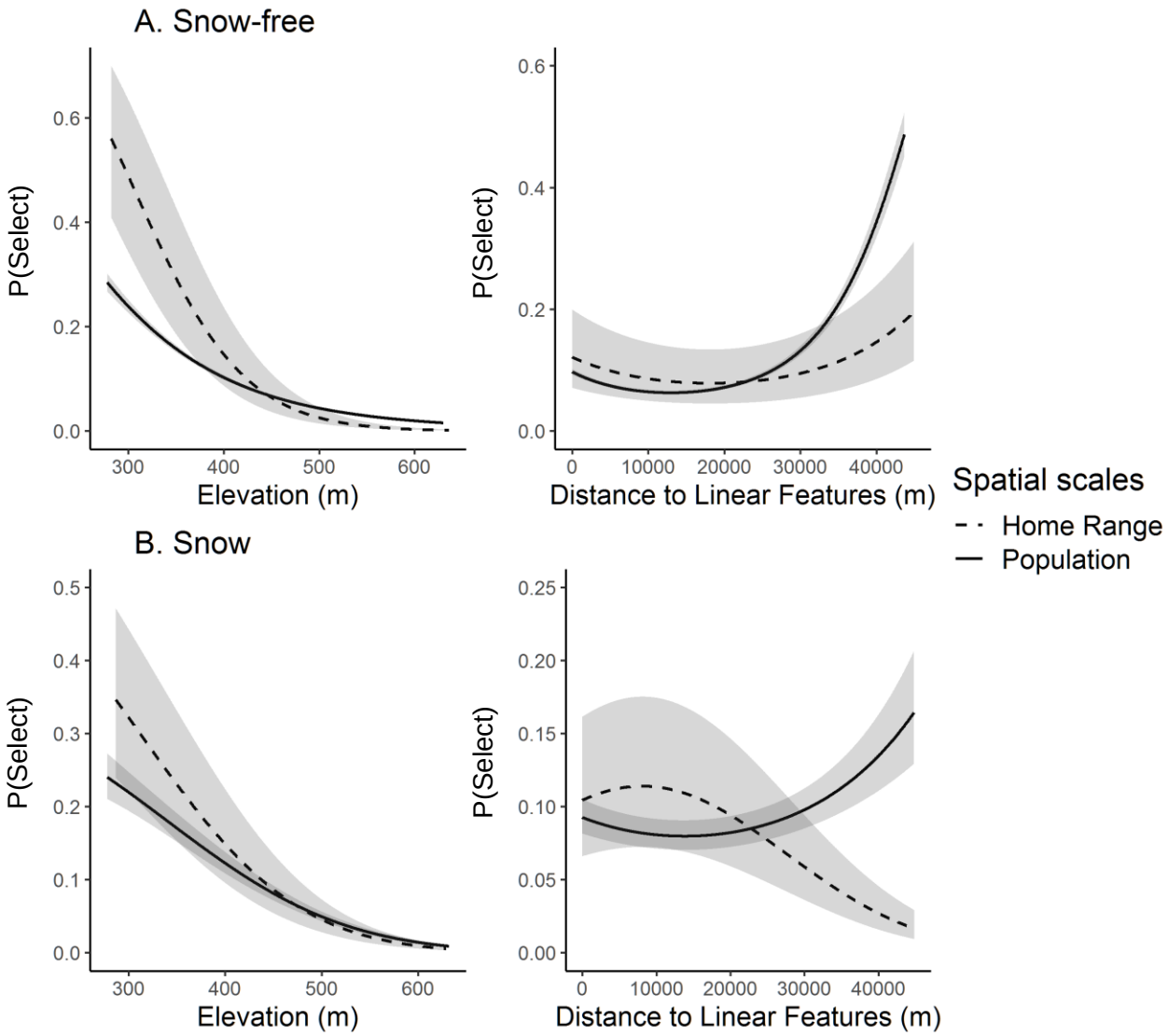

Figure 3.4. Plot of the predicted relative probability of selection (P(Select)) by gray wolves in the Boreal Shield of Saskatchewan as a function of the scaled (centered by the mean and divided by standard deviation) elevation and distance to linear features derived from the top model for each season (A: snow-free and B: snow) and spatial scale. Solid lines represent the population scale and dashed lines represent the home range scale.

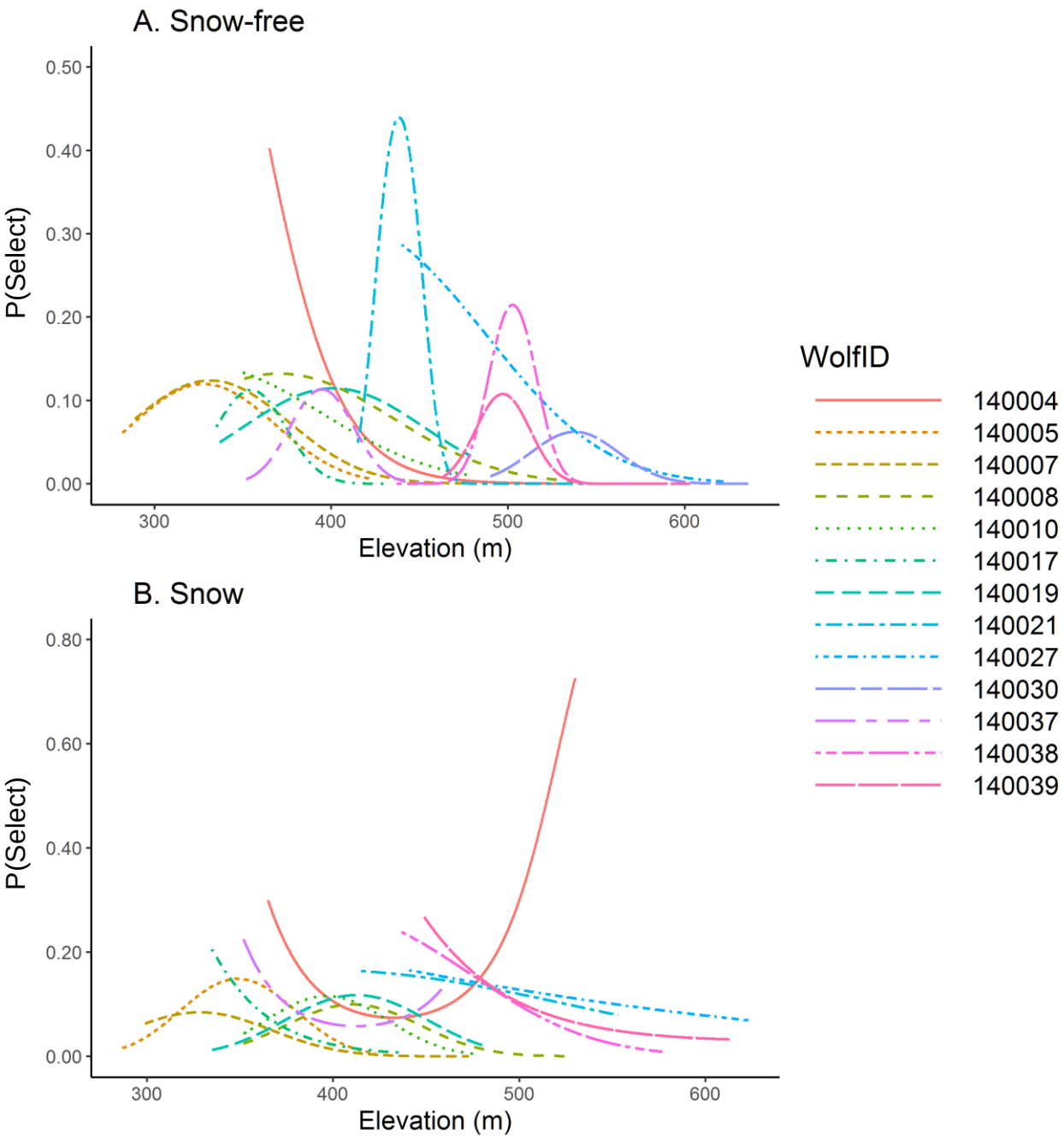

Figure 3.5. Plot of the predicted relative probability of selection (P(Select)) by individual wolves in the Boreal Shield of Saskatchewan as a function of the scaled (centered by the mean and divided by standard deviation) elevation derived from the top model for the snow-free (A) and snow (B) seasons. Each line corresponds to an individual wolf.

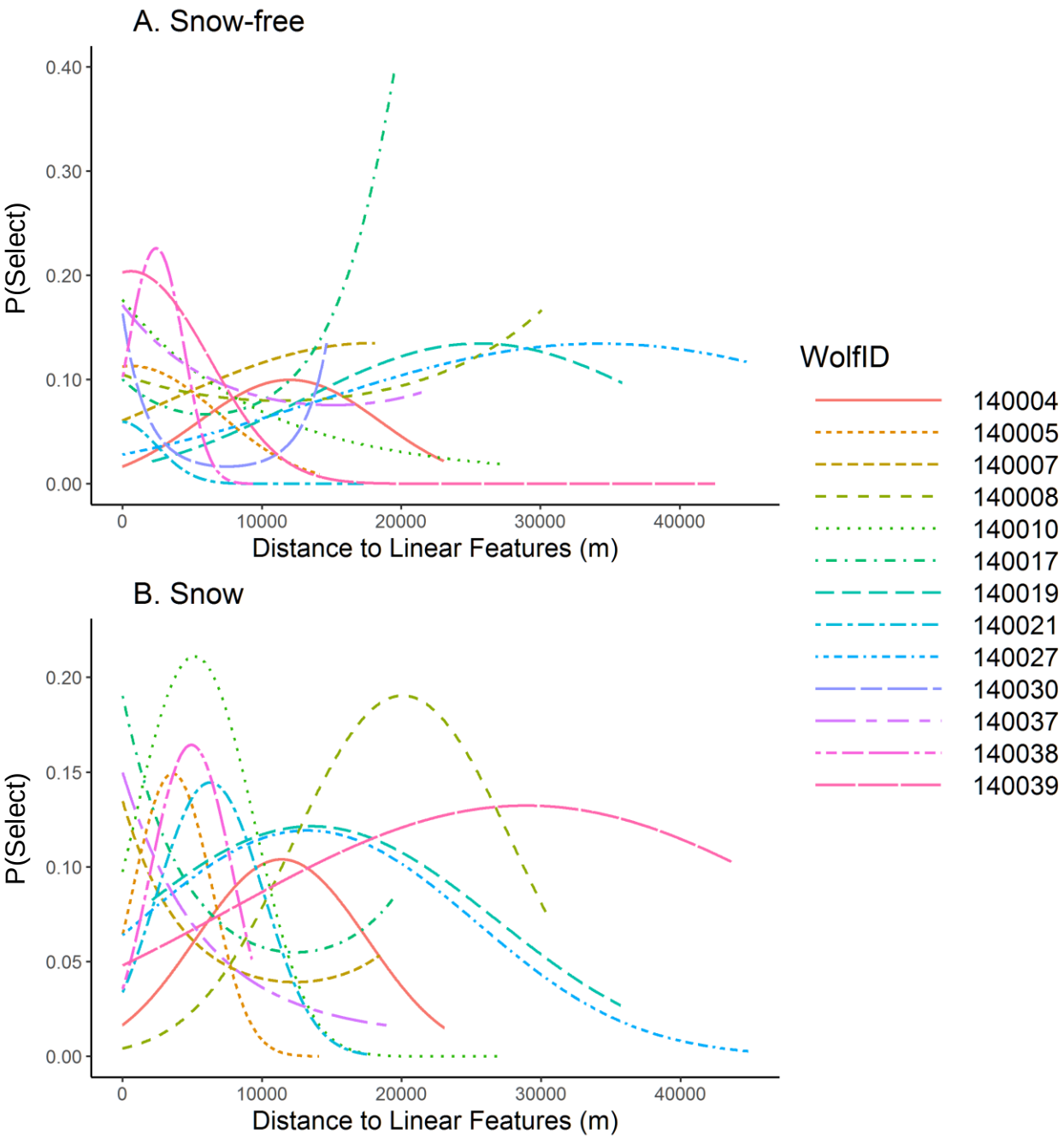

Figure 3.6. Plot of the predicted relative probability of selection (P(Select)) by individual wolves in the Boreal Shield of Saskatchewan as a function of the scaled (centered by the mean and divided by standard deviation) distance to linear features derived from the top model for the snow-free (A) and snow (B) seasons. Each line corresponds to an individual wolf.

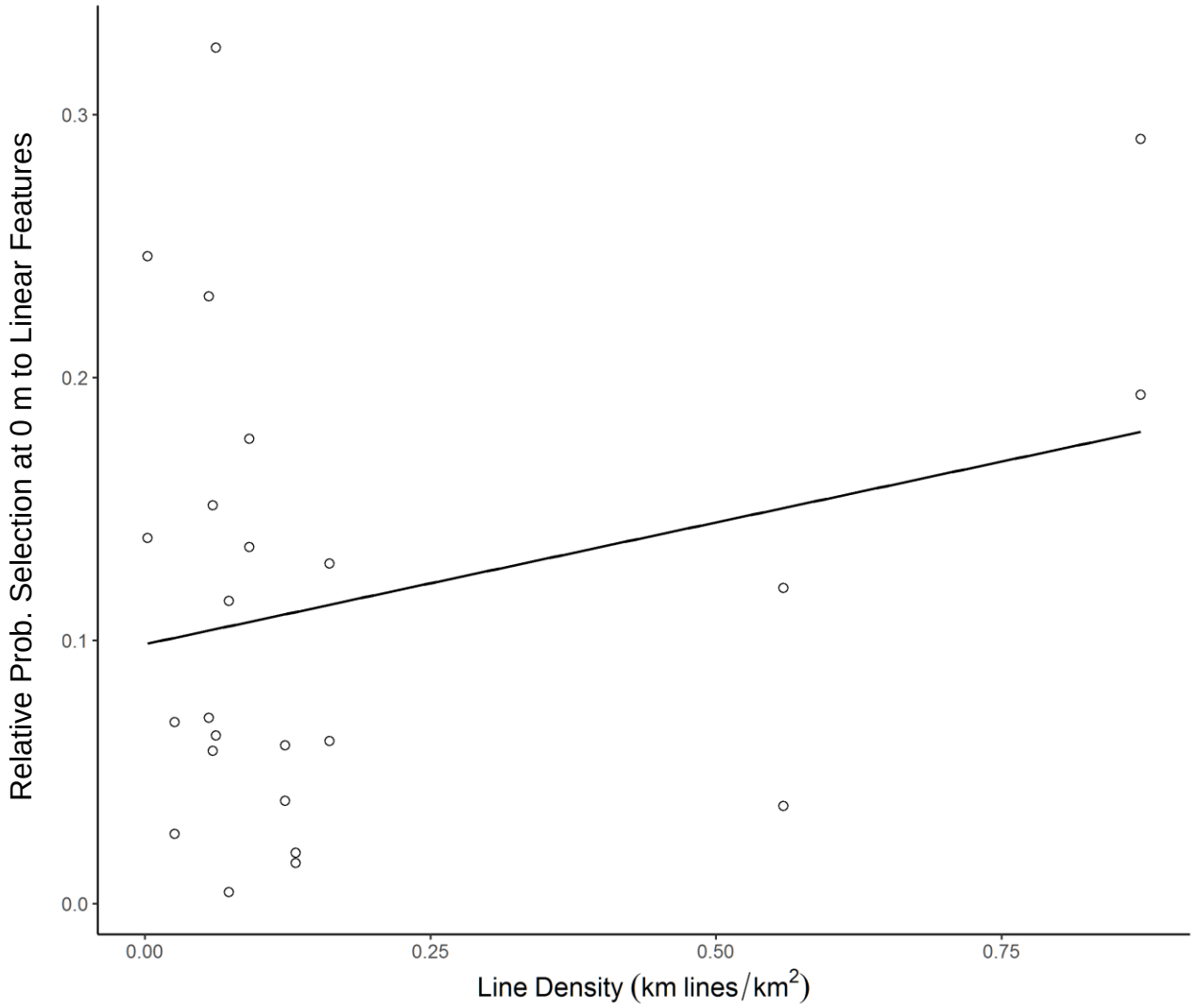

Figure 3.7. Relative probability of selection of linear features as a function of line density in kilometers of lines per square kilometers for wolves in the Boreal Shield of Saskatchewan when distance to linear features is zero meters and all other habitat variables are excluded (R^2 = 0.07, p = 0.21).

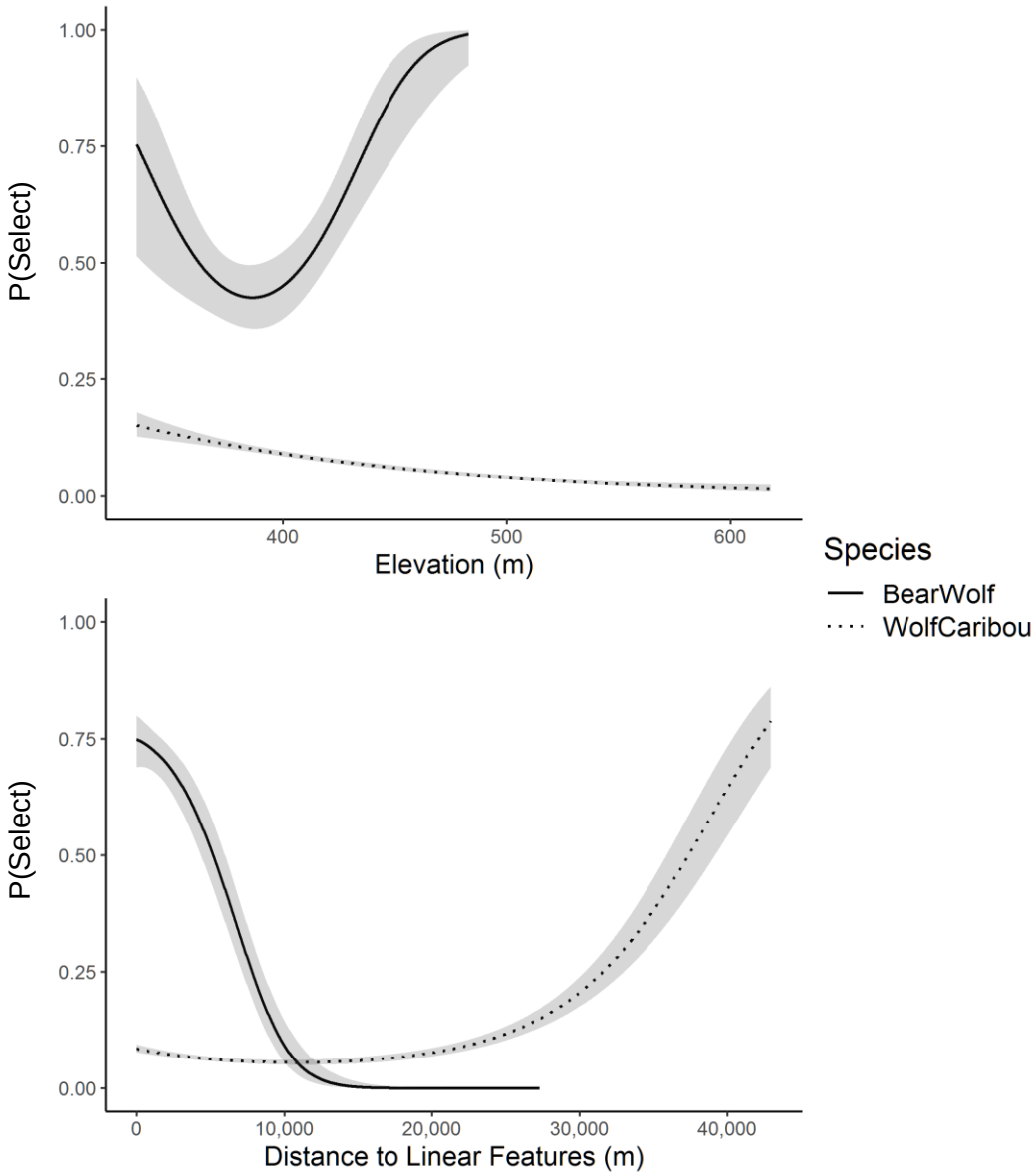

Figure 3.8. Plot of the predicted relative probability of selection (P(Select)) of a resource unit by black bears compared to wolves (solid line) and wolves compared to boreal woodland caribou (dotted line) during the caribou calving and post-calving seasons in the Boreal Shield of Saskatchewan as a function of the scaled (centered by the mean and divided by standard deviation) elevation and distance to linear features derived from the top model.

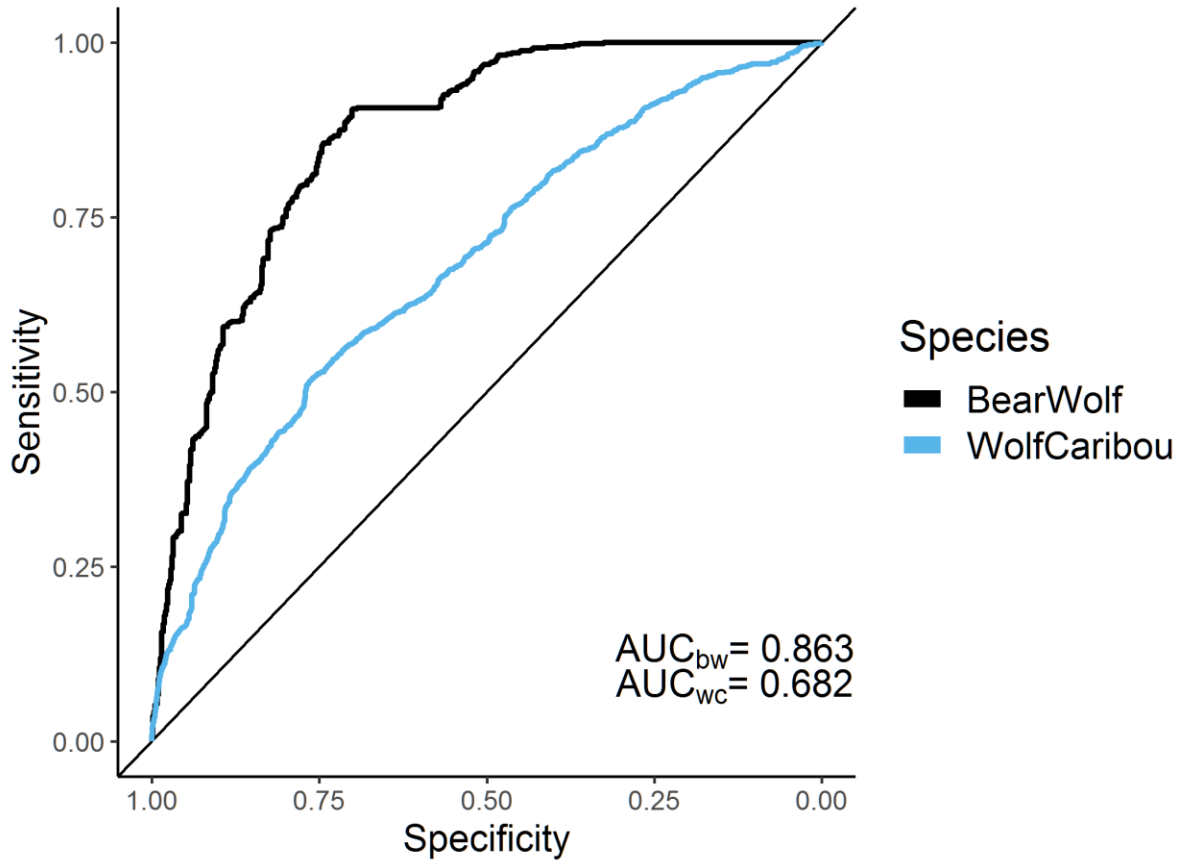

Figure 3.9. Relative operating characteristic curves (ROC) and area under the curve (AUC) for each of two models attempting to assess differential habitat selection of black bears and gray wolves (black line), and gray wolves and boreal woodland caribou (blue line) in the Boreal Shield of Saskatchewan. The straight line represents the case where AUC = 0.5 and the model has no discrimination capacity.

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CHAPTER 4: SUMMARY AND GENERAL CONCLUSIONS

Boreal woodland caribou are listed as Threatened on Schedule 1 of the Canada *Species at Risk Act* (Environment Canada 2012). Their decline has been driven largely by anthropogenic impacts that can be exacerbated by predation (Environment Canada 2012). Much of the research thus far conducted on caribou has occurred in these relatively high human-disturbed habitats (Environment Canada 2012). In the Boreal Shield of Saskatchewan, boreal woodland caribou exist in relatively pristine conditions with low anthropogenic impacts, high fire, and few invasive species (McLoughlin et al. 2019), and as such, the population was assessed designated as "unknown" with respect to self-sustainability (Environment Canada 2012). This thesis was developed as part of a multi-faceted project to assess the current state of the boreal woodland caribou population in the Boreal Shield of Saskatchewan. The initial purpose of my thesis was to understand how predators relate to boreal woodland caribou in the study area. However, upon initial research, it became apparent that very little is known about black bears and wolves in the Boreal Shield of Saskatchewan. Subsequently, the habitat selection analyses of predators not only allows for important comparison to caribou, but also is a pilot work from which future research can build upon. The objectives of my study were to: (i) provide novel information on black bear and wolf ecology in the Boreal Shield of Saskatchewan; (ii) provide a baseline of data from a northern caribou range to which bear-wolf-caribou habitat selection patterns from areas of greater anthropogenic disturbance can be compared; and (iii) examine how the species overlap in habitat selection patterns during the critical calving and post-calving seasons and relate that to potential for predation by black bears relative to wolves.

4.1 Habitat selection of predators in the Boreal Shield of Saskatchewan

Habitat selection is a scale-dependent process that reflects a hierarchy of limiting factors related to fitness (Rettie and Messier 2000). At broader scales, limiting factors include predation (Creel et al. 2005, McLoughlin et al. 2005, Dinkins et al. 2014), competition (Wereszczuk and Zalewski 2015, Duquette et al. 2017), human mortality risk (Basille et al. 2013, Stillfried et al. 2015) and at finer scales the main limiting factor is high quality forage (Fortin et al. 2005, Boyce 2006). Multi-scale habitat selection studies are better able to predict limiting factors for populations and

better inform management and conservation decisions (Wiens 1989, DeCesare et al. 2012). My studies were the first to assess multi-scale habitat selection of black bears and gray wolves in the relatively low human-disturbance and high fire-disturbance landscape of the Boreal Shield of Saskatchewan.

Black bear habitat selection did not vary greatly between scales indicating that limiting factors controlling habitat selection in my study area are prevalent at both the population and home range scales. My results suggest that black bear habitat selection follows forage green-up through the growing season. Forage selection for black bears usually includes grasses, forbs, deciduous plants, and ants during the spring and summer and switch to higher calorie soft- and hard-mast plants in the fall (Mosnier et al. 2008, Romain et al. 2013, Lesmerises et al. 2015). It appears that black bears in Saskatchewan follow this trend selecting for mixed coniferous-deciduous habitat type. Mixed coniferous-deciduous habitat offers a more open canopy that could favour alternate forbs and deciduous plants possibly important for bears in the spring and summer. The shift in relative selection towards young coniferous stands facilitates berry consumption as velvet-leaved blueberry and lingonberry (*Vaccinium myrtilloides*, *Vaccinium vitis-idaea*) were more commonly found and with equal or greater cover in young jack pine stands compared to mature stands, and generally, blueberry occurs more commonly in jack pine stands than it does in any other stand (McLoughlin et al. 2019). Black bears consistently selected for linear features. Likely, this response for black bears was partially a byproduct of the sampling methods with bait sites being stationed around the main highway in the study area.

As a carnivore, wolf habitat selection is one step removed from the landscape, instead wolves generally select for habitat according to prey species availability (Mech and Boitani 2010) and prey habitat (Courbin et al. 2014, Kittle et al. 2017). Therefore, understanding habitat selection patterns of wolves was more complex than that of black bears. In my study area, likely prey for wolves included caribou, moose, and beaver (McLoughlin et al. 2019, Neufeld et al. 2019). Wolves avoided and selected for two important caribou habitats mature black spruce and open muskeg, respectively. Open muskeg could also provide important moose habitat (Timmermann and McNicol 1988, Shipley 2010). Wolf selection of beaver habitat could be indicated by selection of lower elevations or drainages across the landscape. Wolves showed no functional response to linear features as a function of line density. However, I caveat this result with the need for further analysis as these results are preliminary.

Patterns of distribution and resource use can vary at different spatiotemporal scales, which was reflected in my results for both bears and wolves. Substantial variation was also seen within scales especially the individual analyses. Unexpectedly, wolves has greater individual (pack) variation compared to black bears (individuals). Given the opportunistic, omnivorous habits of black bears (Garshelis 2009), it seemed intuitive that they would have weak selection patters, which was true, but that they also would vary between individuals, which was not entirely true. Instead, wolves has greater variability between individual pack habitat selection patterns. However, such patterns were very consistent within individual packs indicating potential for pack specialization.

4.2 Potential for predation on boreal woodland caribou

To understand factors driving caribou populations here, it is important to understand predators of caribou. In other population ranges, wolves are known to be important predators of caribou year-round (McLoughlin et al. 2003, Leblond et al. 2016), but black bears are often implicated in having significant impact on caribou populations through predation of caribou calves (Bergerud 1971, Ballard et al. 1981, Pinard et al. 2012, Mahoney et al. 2016). Caribou can use habitat selection as an anti-predator tactic, especially during calving, to separate from predators (Bergerud et al. 1984). Human disturbance, such as linear features, can cause a breakdown of spatial separation between caribou and wolves as they allow for increased hunting efficiency and encounter rates by wolves (Whittington et al. 2011, Dickie et al. 2017, DeMars and Boutin 2018). Comparing habitat selection patterns can indicate key habitat types that can act as refuges or areas that could have high encounter risk in my study area.

Black bears in my study area, based on my understanding of their relative habitat selection patterns, are not likely to play a significant role in limiting the caribou population through calf predation. Overlap of black bears and caribou during the calving seasons was minimal, and certainly less than that of wolves and caribou. My results suggest that black bears spend the majority of their time foraging in mixed coniferous-deciduous habitat and avoiding calving habitat during critical periods of calf vulnerability. While caribou also appear to successfully spatially separate from wolves during calving season, they do not or cannot do so as strongly as compared to bears and caribou. Hence, I conclude that wolves are likely the more important predator to caribou in the Boreal Shield of Saskatchewan.

4.3 Management implications and future directions

This project was initiated as part of a multi-faceted project to understand the population trends of boreal woodland caribou in the Boreal Shield of Saskatchewan. As such, the purpose of the caribou-related project as a whole was to inform identification of critical habitat for caribou in the Boreal Shield of Saskatchewan. My analysis on predators of caribou not only facilitates an understanding of caribou predation risk, it is also the first to assess important habitat for predators themselves in this area.

In conjunction with the wolf study, Neufeld et al. (In prep) are working to further understand how wolves interact with a variety of prey and the potential for habitat mediated apparent competition with fire as a disturbance type. To understand wolves and bears as predators it would be useful to complete a diet study of both species. Our results suggest that wolves may be the most important predator of caribou and bears maintain their opportunistic-predator status in the Boreal Shield of Saskatchewan, but a diet study could confirm preferences of wolves and bears and further assess the hypothesis that wolves and bears in my study area may specialize on specific prey.

If the purpose of future work is not simply to understand diet but also relate predator and prey habitat selection, then it would be prudent to consider better understanding certain prey habitats. Beaver may be an important prey item to wolves in my study area (Neufeld et al. 2019). Although there are an abundance of waterways across the Boreal Shield, it is wrong to assume they could all be suitable for beaver. Not much is known about beaver habitat selection in central Canada but studies in other regions of North America have found that geomorphology and availability of food are often the most important drivers of beaver habitat (Touihri et al. 2018). However, given the low productivity and deciduous browse in the Boreal Shield, it is difficult to confidently extrapolate potential beaver habitat from vastly different study areas to my study area. Ideally, an analysis of the potential for beaver habitat or a measure of beaver abundance in the area would help to understand available biomass of beaver for wolf diet. Similarly, the same could apply to moose. Although we know that moose density is low in the study area (Neufeld et al. 2019), it is unclear where they find the best forage and refuge to subsist on the landscape.

In Chapter 2, I discuss the potential for bear baiting for hunting to act as a potential diversionary feeding situation that could draw bears away from caribou calves during the spring hunting season. Presence of baits as diversionary feeders have been shown to influence black

bear movement as spring is a time of low forage on the landscape (Garshelis et al. 2017). Baiting for the purposes of hunting occurs widely across most of North America, I strongly suspect that the presence of baits occurs across many black bear ranges and could be unknowingly influencing black bear habitat selection. Simultaneously, studies have shown that bears can assess mortality risk from human hunters and adjust habitat selection patterns to correct for it (Ordiz et al. 2011, Ordiz et al. 2012, Stillfried et al. 2015). Understanding how black bears respond to baits alongside the influence of human mortality risk in an area with low human activity would be an interesting contrast to habitat selection patterns by bears in protected areas or high human activity locations.

Landscape disturbance can exacerbate predation pressure on caribou through habitat mediated apparent competition (Wittmer et al. 2007) or use of linear features as travel and hunting routes (Dickie et al. 2017). Although there is currently no evidence of a strong effect of habitat mediated apparent competition in my study area (Neufeld et al. 2019), with further disturbance it could become an issue for boreal woodland caribou. Similarly, with the potential for a functional response to linear features, a small increase in linear features on the landscape could elicit a disproportional predation response from wolves. This study is useful to compare habitat selection patterns of black bears, wolves, and caribou to patterns in more disturbed areas. It provides useful baseline information that can help to understand the dynamics of a low human-disturbance environment. While it can be an important contrast to high-disturbance studies, it also heeds a warning; we are aware of what the caribou-predator situations are in more disturbed areas, if human expansion continues in the Boreal Shield of Saskatchewan, we can expect to see similar results to those areas.

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Appendix A: Top models and AIC for individual bear RSFs

Table A.1. Comparison of models used to predict resource selection for individual black bears in the Boreal Shield of Saskatchewan. Models are ranked based on Akaike's information criteria (AIC) values. Delta AIC (ΔAIC) measures the difference between each model and the top model and Akaike weights (w_i) indicates the probability that a model is best among an entire set of candidate models. This table is an expanded version of the summary table provided in Table 2.7. Top models for each season are represented in bold font.

		Spring			Summer			Fall		
Bear	Model	AIC	ΔAIC	w_i	AIC	ΔAIC	w_i	AIC	ΔAIC	w_i
3002	Habitat + Elev² + LinDist²	**342.3**	**0**	**0.65**	674.9	4.3	0.06	**216**	**0**	**0.55**
	Habitat + Elev² × LinDist²	344.1	1.8	0.27	676.9	6.3	0.02	216.4	0.4	0.45
	Habitat + Elev + LinDist	347.6	5.3	0.05	672.1	1.5	0.26	226.9	10.9	0.00
	Habitat + Elev × LinDist	348.2	5.9	0.03	673.4	2.8	0.13	228.9	12.9	<0.001
	Habitat	354.7	12.4	0.00	**670.6**	**0**	**0.53**	229.2	13.2	<0.001
3007	Habitat + Elev² × LinDist²	**768.6**	**0**	**0.64**	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
	Habitat + Elev × LinDist	770.2	1.5	0.29	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
	Habitat + Elev + LinDist	773.9	5.3	0.05	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
	Habitat + Elev² + LinDist²	775.4	6.8	0.02	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
	Habitat	789.9	21.2	<0.001	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
3019	Habitat + Elev + LinDist	**266.1**	**0**	**0.53**	1757.4	25.3	<0.001	356.7	6.5	0.03
	Habitat + Elev × LinDist	267.5	1.4	0.26	1738.8	6.6	0.04	358.7	8.5	0.01
	Habitat + Elev² + LinDist²	269.3	3.3	0.10	1750.5	18.4	<0.001	**350.2**	**0**	**0.70**
	Habitat	270.4	4.3	0.06	1780.4	48.3	<0.001	380.8	30.6	<0.001
	Habitat + Elev² × LinDist²	271	5	0.04	**1732.1**	**0**	**0.97**	352.2	2	0.26
3021	Habitat + Elev² × LinDist²	*NA*	*NA*	*NA*	**322**	**0**	**0.89**	**317.5**	**0**	**0.62**

	Habitat + Elev × LinDist	*NA*	*NA*	*NA*	347.3	25.3	<0.001	320.5	3	0.14
	Habitat + Elev² + LinDist²	*NA*	*NA*	*NA*	326.2	4.2	0.11	320.7	3.2	0.13
	Habitat + Elev + LinDist	*NA*	*NA*	*NA*	347.4	25.4	<0.001	320.9	3.4	0.11
	Habitat	*NA*	*NA*	*NA*	371.1	49.1	<0.001	338.4	21	<0.001
3022	Habitat + Elev² + LinDist²	**1110.5**	**0**	**0.41**	1829.5	0.4	0.44	**745.9**	**0**	**0.58**
	Habitat + Elev + LinDist	1111.1	0.7	0.29	1870	40.9	<0.001	774.4	28.5	<0.001
	Habitat + Elev² × LinDist²	1112.4	1.9	0.16	**1829.1**	**0**	**0.56**	746.5	0.6	0.42
	Habitat + Elev × LinDist	1112.5	2	0.15	1869.3	40.3	<0.001	762.1	16.3	<0.001
	Habitat	1136	25.5	<0.001	1872.3	43.2	<0.001	774.3	28.4	<0.001
3023	Habitat + Elev² × LinDist²	**991.9**	**0**	**0.89**	**1317.1**	**0**	**0.99**	**898.7**	**0**	**1.00**
	Habitat + Elev² + LinDist²	996.1	4.2	0.11	1326.8	9.6	0.01	910.2	11.5	0.00
	Habitat + Elev × LinDist	1042.5	50.6	<0.001	1353.2	36.1	<0.001	940.2	41.5	<0.001
	Habitat + Elev + LinDist	1047.9	56	<0.001	1360.3	43.2	<0.001	961.8	63.1	<0.001
	Habitat	1140.1	148.2	<0.001	1637.6	320.5	<0.001	969.5	70.8	<0.001
3029	Habitat + Elev + LinDist	**974.7**	**0**	**0.61**	1765.6	10.4	0.00	1041.8	45.1	<0.001
	Habitat + Elev × LinDist	976.3	1.7	0.26	1763.5	8.2	0.01	1009.6	13	0.00
	Habitat + Elev² + LinDist²	978.4	3.7	0.10	1757.4	2.2	0.25	1027.7	31.1	<0.001
	Habitat + Elev² × LinDist²	980.2	5.6	0.04	**1755.3**	**0**	**0.74**	**996.6**	**0**	**1.00**
	Habitat	1020.8	46.1	<0.001	1809.7	54.4	<0.001	1063.5	66.9	<0.001
3031	Habitat + Elev + LinDist	**1121.8**	**0**	**0.36**	1679.8	36.1	<0.001	970.8	37.6	<0.001
	Habitat + Elev² + LinDist²	1121.9	0.2	0.33	**1643.7**	**0**	**0.73**	937.2	4	0.12
	Habitat + Elev × LinDist	1123.2	1.5	0.17	1674.5	30.8	<0.001	964	30.8	<0.001
	Habitat + Elev² × LinDist²	1123.6	1.8	0.14	1645.6	2	0.27	**933.2**	**0**	**0.88**
	Habitat	1138.1	16.4	<0.001	1696.8	53.1	<0.001	973.7	40.5	<0.001
3035	Habitat + Elev² + LinDist²	*NA*	*NA*	*NA*	635.8	8	0.02	**228**	**0**	**0.64**
	Habitat + Elev² × LinDist²	*NA*	*NA*	*NA*	**627.8**	**0**	**0.83**	229.2	1.2	0.36

	Habitat + Elev × LinDist	*NA*	*NA*	*NA*	631.2	3.3	0.16	247.1	19	<0.001
	Habitat + Elev + LinDist	*NA*	*NA*	*NA*	641.6	13.7	<0.001	247.8	19.7	<0.001
	Habitat	*NA*	*NA*	*NA*	658.1	30.3	<0.001	248.8	20.7	<0.001
3039	Habitat + Elev² + LinDist²	**1066.3**	**0**	**0.56**	**1877.1**	**0**	**0.73**	297.7	0.2	0.48
	Habitat + Elev² × LinDist²	1067.4	1.1	0.32	1879.1	2	0.27	**297.5**	**0**	**0.52**
	Habitat	1071	4.7	0.05	1899	22	<0.001	346.4	48.9	<0.001
	Habitat + Elev + LinDist	1071.5	5.2	0.04	1902.7	25.7	<0.001	341.7	44.2	<0.001
	Habitat + Elev × LinDist	1073.4	7.1	0.02	1903.5	26.5	<0.001	338.1	40.6	<0.001
3053	Habitat + Elev² + LinDist²	**1215.6**	**0**	**0.70**	1861.2	6.4	0.04	*NA*	*NA*	*NA*
	Habitat + Elev² × LinDist²	1217.3	1.7	0.30	**1854.8**	**0**	**0.96**	*NA*	*NA*	*NA*
	Habitat + Elev + LinDist	1235.3	19.7	<0.001	1874.3	19.5	<0.001	*NA*	*NA*	*NA*
	Habitat + Elev × LinDist	1237.3	21.7	<0.001	1876.2	21.4	<0.001	*NA*	*NA*	*NA*
	Habitat	1295.7	80	<0.001	1895.6	40.8	<0.001	1227.7	88.4	<0.001
	Habitat + LinDist + LinDist²	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	**1139.3**	**0**	**1.00**
	Habitat + LinDist	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	1217.7	78.4	<0.001
	Habitat + Elev + Elev²	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	1218.9	79.6	<0.001
	Habitat + Elev	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	1229.7	90.4	<0.001

Appendix B: Individual bear RSF results

Table B.1a. Summary of beta coefficients (β) ± standard error (SE), and *p*-values (*P*) for a subset of variables from generalized linear mixed models predicting seasonal resource selection for individual black bears in the Boreal Shield of Saskatchewan. The table is too large to be displayed in one piece, so it has been truncated to display four variables/terms per table.

		Black Spruce Swamp				Mature Black Spruce				Mature Jack Pine				Mixed Con-Dec			
Season	Bear	β	SE	*P*		β	SE	*P*		β	SE	*P*		β	SE	*P*	
Spring	3002	0.37	0.47	0.42		-14.98	712.03	0.98		-0.28	0.63	0.66		0.28	0.48	0.55	
Spring	3007	-0.42	0.64	0.51		-1.10	0.64	0.09		-0.28	0.58	0.63		-2.37	0.49	0.00	*
Spring	3019	-0.34	0.64	0.60		-2.52	0.46	0.00	*	0.34	0.57	0.55		0.66	0.61	0.28	
Spring	3021	*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*	
Spring	3022	0.09	0.44	0.85		-2.30	0.42	0.00	*	0.29	0.46	0.53	*	0.00	0.50	1.00	
Spring	3023	-0.70	0.34	0.04	*	-0.20	0.26	0.43		-2.56	0.24	< 2e-16	*	-0.55	0.39	0.16	
Spring	3029	-0.30	0.27	0.27		0.09	0.45	0.84		-0.76	0.55	0.17		0.66	0.26	0.01	*
Spring	3031	-1.06	0.60	0.08		-0.07	0.56	0.90		0.18	0.54	0.74		-0.24	0.65	0.71	
Spring	3035	*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*	
Spring	3039	-0.68	0.28	0.01	*	0.15	0.44	0.73		-1.99	0.15	< 2e-16	*	1.24	0.49	0.01	*
Spring	3053	-0.49	0.41	0.24		0.36	0.52	0.49		-0.04	0.43	0.94		0.72	0.43	0.10	
Summer	3002	0.05	0.38	0.90		0.13	0.60	0.83		-0.98	0.58	0.09		0.49	0.33	0.14	
Summer	3007	*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*	
Summer	3019	-1.01	0.33	0.00	*	-0.32	0.33	0.32		-2.60	0.21	< 2e-16	*	0.29	0.25	0.25	
Summer	3021	-0.24	0.53	0.65		-0.71	0.71	0.32		0.16	0.62	0.80		0.41	0.48	0.40	
Summer	3022	-0.36	0.30	0.22		0.05	0.42	0.91		-0.09	0.33	0.77		0.35	0.30	0.24	
Summer	3023	0.36	0.37	0.33		-0.14	0.36	0.69		-0.22	0.36	0.54		-1.09	0.49	0.03	*
Summer	3029	0.41	0.40	0.31		-2.39	0.39	0.00	*	0.41	0.48	0.39		0.55	0.41	0.18	

Summer	3031	0.12	0.22	0.57		-0.77	0.27	0.00	*	-0.40	0.21	0.06		0.21	0.30	0.48	
Summer	3035	0.00	0.47	0.99		0.15	0.63	0.81		-0.22	0.50	0.67		-2.07	0.44	0.00	*
Summer	3039	-0.39	0.19	0.04	*	-0.40	0.43	0.35		-1.94	0.11	< 2e-16	*	0.98	0.47	0.04	*
Summer	3053	-0.34	0.21	0.10		0.22	0.29	0.44		-0.14	0.20	0.49		0.50	0.23	0.03	*
Fall	3002	-1.39	1.20	0.25		-2.39	0.71	0.00	*	0.86	0.71	0.22		-15.35	953.13	0.99	
Fall	3007	*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*	
Fall	3019	-1.37	0.80	0.09		-15.79	1282.18	0.99		0.12	0.72	0.87		-15.38	1069.60	0.99	
Fall	3021	-2.51	0.50	0.00	*	-1.07	1.12	0.34		-0.14	0.75	0.86		-0.77	0.85	0.37	
Fall	3022	-0.47	0.62	0.44		-1.78	0.54	0.00	*	-0.72	0.63	0.26		-0.02	0.63	0.97	
Fall	3023	-0.21	0.35	0.55		-1.63	0.28	0.00	*	-0.73	0.33	0.03	*	-1.25	0.64	0.05	
Fall	3029	-0.70	0.35	0.05	*	-1.09	0.76	0.15		-1.06	0.55	0.05		-0.64	0.37	0.08	
Fall	3031	-0.69	0.42	0.10		-2.12	0.23	< 2e-16	*	-0.33	0.30	0.28		1.49	0.53	0.00	*
Fall	3035	-0.46	0.98	0.64		2.31	1.23	0.06		-2.30	0.89	0.01	*	-0.42	1.32	0.75	
Fall	3039	-1.38	1.16	0.23		1.30	0.82	0.12		0.50	0.57	0.39		-14.34	1952.81	0.99	
Fall	3053	-1.01	0.46	0.03	*	-0.16	0.37	0.66		-1.82	0.20	< 2e-16	*	0.67	0.31	0.03	*

Table B.1b. Summary of beta coefficients (β) ± standard error (SE), and *p*-values (*P*) for a subset of variables from generalized linear mixed models predicting seasonal resource selection for individual black bears in the Boreal Shield of Saskatchewan. The table is too large to be displayed in one piece, so it has been truncated to display four variables/terms per table.

		Open Muskeg				Young-Mid Black Spruce				Young-Mid Jack Pine				Elevation			
Season	Bear	β	SE	*P*		β	SE	*P*		β	SE	P		β	SE	*P*	
Spring	3002	0.26	0.49	0.59		-0.19	0.65	0.76		-3.04	0.46	0.00	*	0.36	0.23	0.11	
Spring	3007	0.57	0.55	0.30		0.62	0.51	0.23		0.15	0.51	0.76		-0.12	0.14	0.37	
Spring	3019	0.52	0.57	0.36		-0.41	0.87	0.64		-0.85	0.86	0.32		-0.48	0.21	0.02	*
Spring	3021	*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*	
Spring	3022	0.14	0.45	0.76		0.49	0.49	0.32		-0.05	0.43	0.91		-0.50	0.12	0.00	*
Spring	3023	-0.24	0.37	0.51		-0.37	0.41	0.37		0.46	0.27	0.09	*	-0.93	0.18	0.00	*
Spring	3029	0.09	0.26	0.72		-0.40	0.34	0.25		-2.47	0.17	< 2e-16	*	-0.57	0.10	0.00	*
Spring	3031	-1.08	0.60	0.07		-2.11	0.53	0.00	*	-1.15	0.79	0.15		-0.24	0.08	0.00	*
Spring	3035	*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*	
Spring	3039	0.73	0.26	0.01	*	-14.21	1668.13	0.99		-13.63	391.30	0.97		-0.11	0.10	0.28	
Spring	3053	-0.37	0.42	0.37		-2.29	0.40	0.00	*	-0.63	0.44	0.15		-0.41	0.11	0.00	*
Summer	3002	-2.21	0.28	0.00	*	-0.64	0.51	0.21		-0.57	0.37	0.12		*NA*	*NA*	*NA*	
Summer	3007	*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*	
Summer	3019	-0.40	0.27	0.14		-0.41	0.28	0.15		0.19	0.22	0.37		-0.15	0.08	0.04	*
Summer	3021	0.30	0.52	0.57		-0.61	0.56	0.27		-2.99	0.49	0.00	*	-1.02	0.32	0.00	*
Summer	3022	0.13	0.30	0.66		-1.78	0.26	0.00	*	-0.02	0.27	0.95		-0.09	0.09	0.29	
Summer	3023	-0.50	0.48	0.30		-3.46	0.36	< 2e-16	*	1.05	0.35	0.00	*	0.09	0.18	0.59	
Summer	3029	0.05	0.40	0.90		0.11	0.43	0.81		0.10	0.40	0.81		-0.29	0.09	0.00	*
Summer	3031	-1.84	0.18	< 2e-16	*	0.75	0.30	0.01	*	1.03	0.22	0.00	*	-0.35	0.10	0.00	*
Summer	3035	0.67	0.46	0.15		0.27	0.63	0.67		0.20	0.47	0.67		-0.07	0.15	0.65	

Summer	3039	0.37	0.24	0.13		-11.52	378.58	0.98		-0.17	0.33	0.61		-0.13	0.08	0.13	
Summer	3053	0.09	0.21	0.67		0.10	0.38	0.80		-1.92	0.17	< 2e-16	*	-0.32	0.09	0.00	*
Fall	3002	-0.93	1.21	0.44		0.69	1.28	0.59		1.76	0.80	0.03	*	0.74	0.29	0.01	*
Fall	3007	*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*	
Fall	3019	-1.85	1.07	0.08		-2.43	0.45	0.00	*	0.46	0.40	0.25		0.02	0.24	0.92	
Fall	3021	-0.42	0.68	0.54		0.52	0.55	0.34		1.00	0.50	0.04	*	-0.68	0.28	0.02	*
Fall	3022	0.07	0.65	0.91		0.32	0.69	0.64		0.70	0.55	0.20		-0.14	0.14	0.34	
Fall	3023	0.35	0.44	0.43		-0.35	0.36	0.34		-0.04	0.32	0.91		0.33	0.16	0.04	*
Fall	3029	-0.70	0.35	0.04	*	-1.77	0.23	0.00	*	0.23	0.22	0.30		0.10	0.11	0.36	
Fall	3031	0.77	0.30	0.01	*	1.49	0.41	0.00	*	1.69	0.31	0.00	*	-0.03	0.12	0.82	
Fall	3035	-0.29	1.09	0.79		-15.79	1055.25	0.99		0.89	0.85	0.30		1.35	0.41	0.00	*
Fall	3039	-13.81	847.35	0.99		-14.92	2786.47	1.00		-1.80	0.55	0.00	*	0.72	0.23	0.00	*
Fall	3053	0.54	0.33	0.10		-0.88	0.62	0.16		0.74	0.22	0.00	*	0.35	0.13	0.01	*

Table B.1c. Summary of beta coefficients (β) ± standard error (SE), and *p*-values (*P*) for a subset of variables from generalized linear mixed models predicting seasonal resource selection for individual black bears in the Boreal Shield of Saskatchewan. The table is too large to be displayed in one piece, so it has been truncated to display four variables/terms per table.

		Elevation^2				LinDist				LinDist^2				Elevation x LinDist			
Season	Bear	β	SE	*P*		β	SE	*P*		β	SE	*P*		β	SE	*P*	
Spring	3002	-0.14	0.15	0.35		-0.78	0.21	0.00	*	0.62	0.20	0.00	*	*NA*	*NA*	*NA*	
Spring	3007	-0.29	0.14	0.03	*	0.28	0.14	0.04	*	-0.01	0.12	0.92		-0.42	0.15	0.01	*
Spring	3019	*NA*	*NA*	*NA*		-0.32	0.21	0.12		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*	
Spring	3021	*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*	
Spring	3022	-0.13	0.07	0.08		-0.10	0.11	0.37		-0.09	0.09	0.31		*NA*	*NA*	*NA*	
Spring	3023	-0.54	0.10	0.00	*	-1.35	0.15	< 2e-16	*	0.30	0.09	0.00	*	-0.44	0.18	0.01	*
Spring	3029	*NA*	*NA*	*NA*		-0.44	0.09	0.00	*	*NA*	*NA*	*NA*		*NA*	*NA*	*NA*	
Spring	3031	*NA*	*NA*	*NA*		-0.33	0.09	0.00	*	*NA*	*NA*	*NA*		*NA*	*NA*	*NA*	
Spring	3035	*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*	
Spring	3039	-0.25	0.10	0.01	*	-0.11	0.12	0.38		-0.11	0.09	0.26		*NA*	*NA*	*NA*	
Spring	3053	-0.31	0.11	0.01	*	-0.52	0.09	0.00	*	0.28	0.07	0.00	*	*NA*	*NA*	*NA*	
Summer	3002	*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*	
Summer	3007	*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*	
Summer	3019	0.09	0.05	0.08		-0.39	0.09	0.00	*	0.26	0.08	0.00	*	0.39	0.09	0.00	*
Summer	3021	-0.75	0.25	0.00	*	-1.40	0.25	0.00	*	0.70	0.18	0.00	*	-0.71	0.30	0.02	*
Summer	3022	-0.34	0.08	0.00	*	-0.08	0.08	0.32		-0.32	0.08	0.00	*	0.17	0.11	0.12	
Summer	3023	-0.28	0.06	0.00	*	-1.86	0.14	< 2e-16	*	0.53	0.11	0.00	*	0.65	0.19	0.00	*
Summer	3029	-0.25	0.08	0.00	*	-0.28	0.09	0.00	*	-0.04	0.08	0.63		0.19	0.10	0.04	*
Summer	3031	-0.31	0.08	0.00	*	0.13	0.09	0.18		-0.34	0.09	0.00	*	*NA*	*NA*	*NA*	
Summer	3035	-0.14	0.12	0.25		-0.36	0.14	0.01	*	-0.38	0.16	0.02	*	0.54	0.16	0.00	*

Summer	3039	-0.37	0.08	0.00	*	-0.01	0.09	0.93		-0.01	0.05	0.84		*NA*	*NA*	*NA*	
Summer	3053	-0.43	0.10	0.00	*	0.05	0.09	0.56		-0.16	0.09	0.07		0.29	0.10	0.01	*
Fall	3002	0.22	0.18	0.22		-0.61	0.35	0.09		-1.23	0.38	0.00	*	*NA*	*NA*	*NA*	
Fall	3007	*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*	
Fall	3019	-0.57	0.22	0.01	*	-1.44	0.47	0.00	*	-0.21	0.48	0.66		*NA*	*NA*	*NA*	
Fall	3021	-0.50	0.23	0.03	*	-1.00	0.32	0.00	*	-0.22	0.26	0.40		-0.65	0.32	0.04	*
Fall	3022	-0.38	0.14	0.01	*	0.15	0.14	0.25		-0.56	0.14	0.00	*	*NA*	*NA*	*NA*	
Fall	3023	-0.89	0.16	0.00	*	-0.41	0.13	0.00	*	0.05	0.11	0.67		0.59	0.17	0.00	*
Fall	3029	0.04	0.10	0.69		-0.42	0.13	0.00	*	-0.50	0.14	0.00	*	-0.73	0.12	0.00	*
Fall	3031	-0.53	0.12	0.00	*	-0.33	0.11	0.00	*	-0.24	0.10	0.02	*	-0.30	0.12	0.02	*
Fall	3035	-1.24	0.40	0.00	*	0.26	0.23	0.26		0.03	0.19	0.86		*NA*	*NA*	*NA*	
Fall	3039	-0.12	0.15	0.43		1.13	0.36	0.00	*	-1.94	0.43	0.00	*	0.55	0.40	0.17	
Fall	3053	-1.09	0.14	0.00	*	*NA*	*NA*	*NA*		*NA*	*NA*	*NA*		*NA*	*NA*	*NA*	

Table B.2. Summary table of sex and age of individual black bears analyzed in generalized linear mixed models predicting seasonal resource selection for individual black bears in the Boreal Shield of Saskatchewan.

Bear	**Sex**	**Age**
3002	M	Sub-adult
3007	F	Sub-adult
3019	Unknown	Unknown
3021	M	Sub-adult
3022	F	Adult
3023	M	Adult
3029	F	Sub-adult
3031	F	Sub-adult
3035	M	Sub-adult
3039	F	Adult
3053	F	Sub-adult

Appendix C: Top models and AID for individual wolf RSFs

Table C.1. Comparison of models used to predict resource selection for individual wolves (i.e. packs) in the Boreal Shield of Saskatchewan. Models are ranked based on Akaike's information criteria (AIC) values. Delta AIC (ΔAIC) measures the difference between each model and the top model and Akaike weights (w_i) indicates the probability that a model is best among an entire set of candidate models. This table is an expanded version of the summary table provided in Table 3.7. Top models for each season are represented in bold font.

		Snow-free			Snow		
Wolf	Model	AIC	ΔAIC	w_i	AIC	ΔAIC	w_i
140004	Habitat + Elevation² + LinDist²	**13541.6**	**0**	**0.68**	**8671.9**	**0**	**0.73**
	Habitat + Elevation² × LinDist²	13543.1	1.5	0.32	8673.9	2	0.27
	Habitat + Elevation × LinDist	13754	212.4	<0.001	9085.9	414	<0.001
	Habitat + Elevation + LinDist	13794.1	252.4	<0.001	9103.7	431.8	<0.001
	Habitat	15369.5	1827.9	<0.001	9158.6	486.7	<0.001
140005	Habitat + Elevation² × LinDist²	**14872.8**	**0**	**1**	**8107.8**	**0**	**1**
	Habitat + Elevation × LinDist	14954.8	82	<0.001	8419.2	311.4	<0.001
	Habitat + Elevation² + LinDist²	14999.3	126.5	<0.001	8214.7	106.9	<0.001
	Habitat + Elevation + LinDist	15015.6	142.8	<0.001	8420.8	313	<0.001
	Habitat	15156.2	283.4	<0.001	8461.3	353.5	<0.001
140007	Habitat + Elevation² + LinDist²	**7596.7**	**0**	**0.72**	7595.9	146.9	<0.001
	Habitat + Elevation² × LinDist²	7598.6	1.9	0.28	**7449**	**0**	**1**
	Habitat + Elevation + LinDist	7652.3	55.6	<0.001	7663.1	214.1	<0.001
	Habitat + Elevation × LinDist	7652.8	56.1	<0.001	7511.2	62.2	<0.001
	Habitat	7863.9	267.2	<0.001	8714.4	1265.4	<0.001
140008	Habitat + Elevation² × LinDist²	**11023**	**0**	**0.79**	**7398.2**	**0**	**1**

	Habitat + Elevation² + LinDist²	11025.6	2.6	0.21	7466.3	68	<0.001
	Habitat + Elevation + LinDist	11082.4	59.4	<0.001	7780.7	382.4	<0.001
	Habitat + Elevation × LinDist	11083.4	60.4	<0.001	7741.3	343.1	<0.001
	Habitat	11399.4	376.4	<0.001	9071.3	1673.1	<0.001
140010	Habitat + Elevation² + LinDist²	**14386.9**	**0**	**0.572**	**7590.4**	**0**	**0.54**
	Habitat + Elevation² × LinDist²	14387.6	0.8	0.387	7590.7	0.3	0.46
	Habitat + Elevation × LinDist	14393.5	6.6	0.021	8043	452.6	<0.001
	Habitat + Elevation + LinDist	14393.6	6.7	0.02	8062.4	472.1	<0.001
	Habitat	15454.4	1067.6	<0.001	8848.8	1258.4	<0.001
140017	Habitat + Elevation² × LinDist²	**6886.9**	**0**	**0.987**	**5945.8**	**0**	**1**
	Habitat + Elevation² + LinDist²	6895.6	8.6	0.013	6099	153.2	<0.001
	Habitat + Elevation + LinDist	7092.3	205.3	<0.001	6103.1	157.3	<0.001
	Habitat + Elevation × LinDist	7093.9	207	<0.001	5963.4	17.6	<0.001
	Habitat	7447.2	560.3	<0.001	6413.2	467.4	<0.001
140019	Habitat + Elevation² × LinDist²	**7673.2**	**0**	**0.83**	**6018.5**	**0**	**0.71**
	Habitat + Elevation² + LinDist²	7676.3	3.1	0.17	6020.3	1.8	0.29
	Habitat + Elevation × LinDist	7707.5	34.3	<0.001	6072.6	54.1	<0.001
	Habitat + Elevation + LinDist	7770.2	97	<0.001	6082.8	64.3	<0.001
	Habitat	7859	185.8	<0.001	6154.2	135.6	<0.001
140021	Habitat + Elevation² × LinDist²	**4577.4**	**0**	**1**	4462.5	1.8	0.29
	Habitat + Elevation² + LinDist²	4712.2	134.8	<0.001	**4460.7**	**0**	**0.71**
	Habitat + Elevation × LinDist	5062.5	485.1	<0.001	4663.4	202.7	<0.001
	Habitat + Elevation + LinDist	5085.2	507.8	<0.001	4662.5	201.8	<0.001
	Habitat	6544.6	1967.2	<0.001	4702.4	241.7	<0.001
140027	Habitat + Elevation² × LinDist²	**7705.6**	**0**	**1**	**5286.6**	**0**	**0.936**
	Habitat + Elevation² + LinDist²	7722.2	16.5	<0.001	5291.9	5.4	0.064

	Habitat + Elevation × LinDist	7732.2	26.6	<0.001	5376.2	89.6	<0.001
	Habitat + Elevation + LinDist	7733.2	27.6	<0.001	5374.2	87.6	<0.001
	Habitat	8081.6	376	<0.001	5505.9	219.4	<0.001
140030	Habitat + Elevation² × LinDist²	**7142.7**	**0**	**1**	1634.3	0.2	0.305
	Habitat + Elevation² + LinDist²	7168.6	25.9	<0.001	**1634.1**	**0**	**0.343**
	Habitat + Elevation × LinDist	7474.8	332.1	<0.001	1636.6	2.6	0.095
	Habitat + Elevation + LinDist	7507.7	365	<0.001	1634.7	0.6	0.257
	Habitat	7734.8	592.1	<0.001	1680.4	46.4	<0.001
140037	Habitat + Elevation² × LinDist²	**6719.5**	**0**	**1**	**4065.8**	**0**	**0.997**
	Habitat + Elevation² + LinDist²	6772.6	53.1	<0.001	4077.4	11.6	0.0029
	Habitat + Elevation × LinDist	7012.6	293.1	<0.001	4088.4	22.6	<0.001
	Habitat + Elevation + LinDist	7032.9	313.4	<0.001	4094	28.3	<0.001
	Habitat	7210.6	491.1	<0.001	4291	225.3	<0.001
140038	Habitat + Elevation² × LinDist²	**7386.6**	**0**	**0.9965**	**3842.6**	**0**	**1**
	Habitat + Elevation² + LinDist²	7397.9	11.3	0.0035	3887.5	44.9	<0.001
	Habitat + Elevation + LinDist	8294.6	908	<0.001	3916	73.4	<0.001
	Habitat + Elevation × LinDist	8296	909.5	<0.001	3873.6	31	<0.001
	Habitat	8310.9	924.3	<0.001	4085.6	243	<0.001
140039	Habitat + Elevation² × LinDist²	**7019.3**	**0**	**1**	**7776.9**	**0**	**0.936**
	Habitat + Elevation² + LinDist²	7070.3	51.1	<0.001	7782.3	5.4	0.064
	Habitat + Elevation × LinDist	7434.9	415.6	<0.001	7795.3	18.4	<0.001
	Habitat + Elevation + LinDist	7437.2	417.9	<0.001	7801.5	24.6	<0.001
	Habitat	8122.4	1103.1	<0.001	7961.8	184.9	<0.001

Appendix D: Individual wolf RSF results

Table D.1a. Summary of beta coefficients (β) ± standard error (SE), and *p*-values (*P*) for a subset of variables from generalized linear mixed models predicting seasonal resource selection for individual wolves in the Boreal Shield of Saskatchewan. Significant negative and positive coefficients are highlighted in yellow and blue, respectively. Intercepts are highlighted in grey. The table is too large to be displayed in one piece, so it has been truncated to display four variables/terms per table.

		Black Spruce Swamp				Mature Black Spruce				Mature Jack Pine				Mixed Con-Dec			
Season	Wolf	β	SE	*P*		β	SE	*P*		β	SE	*P*		β	SE	*P*	
Snow-free	140004	0.398	0.085	<0.001	*	-0.603	0.093	<0.001	*	0.228	0.094	0.016	*	-2.583	0.072	<0.001	*
Snow-free	140005	0.367	0.084	<0.001	*	-0.177	0.091	0.052		-0.196	0.095	0.040	*	0.329	0.083	<0.001	*
Snow-free	140007	0.434	0.119	<0.001	*	-0.512	0.122	<0.001	*	-0.039	0.128	0.762		-2.351	0.094	<0.001	*
Snow-free	140008	-0.063	0.101	0.531		0.511	0.123	<0.001	*	0.194	0.104	0.062		-2.453	0.085	<0.001	*
Snow-free	140010	-0.098	0.097	0.314		-0.418	0.121	<0.001	*	0.152	0.095	0.110		0.035	0.112	0.752	
Snow-free	140017	0.247	0.118	0.036	*	-0.892	0.110	<0.001	*	0.356	0.105	<0.001	*	-2.272	0.090	<0.001	*
Snow-free	140019	-0.112	0.138	0.416		0.156	0.203	0.443		-0.620	0.182	<0.001	*	0.375	0.150	0.013	*
Snow-free	140021	0.032	0.101	0.752		1.617	0.192	<0.001	*	-0.082	0.124	0.506		0.358	0.259	0.167	
Snow-free	140027	-0.124	0.184	0.500		-2.365	0.166	<0.001	*	0.245	0.164	0.137		0.588	0.198	0.003	*
Snow-free	140030	0.229	0.391	0.559		1.909	0.409	<0.001	*	-0.226	0.383	0.556		-1.269	1.095	0.247	
Snow-free	140037	0.000	0.150	0.998		-2.339	0.135	<0.001	*	0.886	0.136	<0.001	*	-0.714	0.241	0.003	*
Snow-free	140038	-0.378	0.111	<0.001	*	-0.070	0.228	0.759		-1.264	0.068	<0.001	*	0.113	0.351	0.749	
Snow-free	140039	-0.142	0.210	0.498		-0.021	0.302	0.945		-0.524	0.204	0.010	*	-1.119	0.433	0.010	*
Snow	140004	0.644	0.102	<0.001	*	-0.894	0.118	<0.001	*	-0.072	0.111	0.516		-0.016	0.108	0.882	
Snow	140005	0.042	0.133	0.749		-0.034	0.126	0.785		0.636	0.108	<0.001	*	0.093	0.126	0.462	
Snow	140007	-0.234	0.130	0.072		-2.845	0.080	<0.001	*	0.327	0.097	<0.001	*	0.771	0.088	<0.001	*
Snow	140008	-2.418	0.080	<0.001	*	-0.245	0.194	0.207		-0.580	0.169	<0.001	*	0.230	0.104	0.027	*
Snow	140010	-0.117	0.124	0.344		0.306	0.139	0.027	*	-2.511	0.100	<0.001	*	1.223	0.116	<0.001	*

Snow	140017	-0.039	0.125	0.754		-2.725	0.080	<0.001	*	0.070	0.108	0.514		0.789	0.094	<0.001	*
Snow	140019	-2.009	0.086	<0.001	*	-0.732	0.305	0.016	*	-0.865	0.177	<0.001	*	0.496	0.126	<0.001	*
Snow	140021	0.234	0.297	0.431		-1.713	0.290	<0.001	*	-0.199	0.305	0.514		0.539	0.363	0.137	
Snow	140027	0.046	0.146	0.750		-0.243	0.251	0.334		0.426	0.119	<0.001	*	0.560	0.162	<0.001	*
Snow	140030	-2.380	0.249	<0.001	*	0.400	0.592	0.499		-0.057	0.242	0.813		-14.157	819.128	0.986	
Snow	140037	-0.349	0.172	0.042	*	0.495	0.172	0.004	*	-3.013	0.131	<0.001	*	0.967	0.170	<0.001	*
Snow	140038	-0.181	0.186	0.330		0.248	0.287	0.388		-0.247	0.170	0.146		-0.359	0.623	0.564	
Snow	140039	0.067	0.106	0.526		-0.010	0.241	0.967		-2.146	0.072	<0.001	*	0.216	0.192	0.262	

Table D.1b. Summary of beta coefficients (β) ± standard error (SE), and *p*-values (*P*) for a subset of variables from generalized linear mixed models predicting seasonal resource selection for individual wolves in the Boreal Shield of Saskatchewan. Significant negative and positive coefficients are highlighted in yellow and blue, respectively. Intercepts are highlighted in grey. The table is too large to be displayed in one piece, so it has been truncated to display four variables/terms per table.

		Open Muskeg				Young-Mid Black Spruce				Young-Mid Jack Pine				Elevation			
Season	Wolf	β	SE	*P*		β	SE	*P*		β	SE	*P*		β	SE	*P*	
Snow-free	140004	0.598	0.085	<0.001	*	0.659	0.086	<0.001	*	0.155	0.098	0.114		-1.157	0.041	<0.001	*
Snow-free	140005	0.585	0.080	<0.001	*	-2.216	0.055	<0.001	*	-0.248	0.066	<0.001	*	-0.385	0.030	<0.001	*
Snow-free	140007	0.775	0.120	<0.001	*	0.242	0.119	0.042	*	0.495	0.109	<0.001	*	-0.535	0.043	<0.001	*
Snow-free	140008	0.073	0.101	0.470		0.293	0.118	0.013	*	-0.214	0.097	0.028	*	-0.538	0.035	<0.001	*
Snow-free	140010	0.084	0.094	0.367		-2.513	0.087	<0.001	*	-0.258	0.095	0.006	*	-0.448	0.032	<0.001	*
Snow-free	140017	0.517	0.113	<0.001	*	-0.757	0.152	<0.001	*	-0.325	0.167	0.052		-0.957	0.056	<0.001	*
Snow-free	140019	0.183	0.136	0.177		-2.055	0.125	<0.001	*	0.074	0.133	0.574		-0.025	0.038	0.504	
Snow-free	140021	0.437	0.119	<0.001	*	-0.956	0.272	<0.001	*	-4.920	0.212	<0.001	*	-7.196	0.392	<0.001	*
Snow-free	140027	-0.094	0.181	0.602		0.319	0.216	0.140		0.007	0.167	0.967		-0.763	0.045	<0.001	*
Snow-free	140030	-0.784	0.416	0.059		-2.337	0.382	<0.001	*	-0.784	0.386	0.043	*	-0.234	0.056	<0.001	*
Snow-free	140037	0.026	0.151	0.861		0.441	0.172	0.010	*	0.055	0.150	0.715		-0.609	0.062	<0.001	*
Snow-free	140038	-0.148	0.118	0.211		0.466	0.169	0.006	*	0.005	0.074	0.942		-0.313	0.064	<0.001	*
Snow-free	140039	-0.701	0.222	0.002	*	-2.366	0.205	<0.001	*	-0.066	0.193	0.732		-1.425	0.142	<0.001	*
Snow	140004	0.409	0.110	<0.001	*	-0.244	0.131	0.062		-2.265	0.086	<0.001	*	-0.350	0.032	<0.001	*
Snow	140005	0.292	0.127	0.021	*	-1.868	0.077	<0.001	*	0.020	0.086	0.813		-0.139	0.039	<0.001	*
Snow	140007	0.231	0.125	0.066		-0.158	0.122	0.196		-0.565	0.119	<0.001	*	-0.752	0.053	<0.001	*
Snow	140008	0.687	0.093	<0.001		0.208	0.126	0.099		-0.294	0.096	0.002	*	-0.590	0.062	<0.001	*
Snow	140010	0.738	0.104	<0.001	*	0.383	0.142	0.007	*	0.438	0.106	<0.001	*	-0.246	0.046	<0.001	*
Snow	140017	0.193	0.119	0.104		-1.013	0.182	<0.001	*	-1.153	0.249	<0.001	*	-0.727	0.049	<0.001	*

Snow	140019	0.524	0.096	<0.001	*	0.045	0.147	0.760		-0.341	0.107	0.001	*	0.198	0.045	<0.001	
Snow	140021	1.111	0.294	<0.001	*	0.515	0.332	0.121		-0.661	0.295	0.025	*	-0.122	0.044	0.005	*
Snow	140027	-2.032	0.109	<0.001	*	-0.601	0.293	0.040	*	-0.325	0.121	0.007	*	-0.162	0.047	<0.001	*
Snow	140030	0.096	0.341	0.778		-14.257	540.862	0.979		-0.435	0.257	0.090		-0.080	0.089	0.369	
Snow	140037	0.537	0.140	<0.001	*	0.438	0.179	0.015	*	0.333	0.145	0.021	*	-0.165	0.050	<0.001	*
Snow	140038	-2.326	0.143	<0.001	*	0.017	0.301	0.955		0.189	0.151	0.209		-0.526	0.057	<0.001	*
Snow	140039	0.363	0.097	<0.001	*	-0.054	0.172	0.753		-0.550	0.081	<0.001	*	-0.375	0.036	<0.001	*

Table D.1c. Summary of beta coefficients (β) ± standard error (SE), and *p*-values (*P*) for a subset of variables from generalized linear mixed models predicting seasonal resource selection for individual wolves in the Boreal Shield of Saskatchewan. The table is too large to be displayed in one piece, so it has been truncated to display four variables/terms per table.

		Elevation^2				LinDist				LinDist^2				Elevation x LinDist			
Season	Wolf	β	SE	*P*		β	SE	*P*		β	SE	*P*		β	SE	*P*	
Snow-free	140004	-0.016	0.029	0.573		0.674	0.034	<0.001	*	-0.392	0.027	<0.001	*	*NA*	*NA*	*NA*	
Snow-free	140005	-0.154	0.023	<0.001	*	-0.302	0.031	<0.001	*	-0.130	0.023	<0.001	*	-0.324	0.031	<0.001	*
Snow-free	140007	-0.248	0.038	<0.001	*	0.258	0.036	<0.001	*	-0.043	0.031	0.168		*NA*	*NA*	*NA*	
Snow-free	140008	-0.131	0.023	<0.001	*	-0.061	0.033	0.063		0.112	0.022	<0.001	*	0.072	0.033	0.032	*
Snow-free	140010	-0.063	0.024	0.008	*	-0.638	0.030	<0.001	*	0.044	0.027	0.113		*NA*	*NA*	*NA*	
Snow-free	140017	-0.539	0.050	<0.001	*	0.368	0.038	<0.001	*	0.228	0.032	<0.001	*	0.153	0.048	0.001	*
Snow-free	140019	-0.163	0.037	<0.001	*	0.364	0.041	<0.001	*	-0.178	0.042	<0.001	*	0.110	0.048	0.022	*
Snow-free	140021	-2.799	0.176	<0.001	*	-3.588	0.292	<0.001	*	-1.525	0.131	<0.001	*	-2.522	0.252	<0.001	*
Snow-free	140027	-0.097	0.040	0.015	*	0.621	0.050	<0.001	*	-0.231	0.043	<0.001	*	0.255	0.061	<0.001	*
Snow-free	140030	-0.560	0.051	<0.001	*	-1.244	0.083	<0.001	*	0.287	0.031	<0.001	*	0.413	0.077	<0.001	*
Snow-free	140037	-0.737	0.051	<0.001	*	-0.312	0.040	<0.001	*	0.075	0.039	0.052		0.412	0.060	<0.001	*
Snow-free	140038	-1.401	0.079	<0.001	*	0.393	0.048	<0.001	*	-0.461	0.042	<0.001	*	0.299	0.082	<0.001	*
Snow-free	140039	-1.020	0.072	<0.001	*	-2.803	0.287	<0.001	*	-1.571	0.279	<0.001	*	-1.403	0.204	<0.001	*
Snow	140004	0.247	0.015	<0.001	*	0.665	0.044	<0.001	*	-0.451	0.034	<0.001	*	*NA*	*NA*	*NA*	
Snow	140005	-0.273	0.035	<0.001	*	-0.239	0.046	<0.001	*	-0.664	0.051	<0.001	*	-0.553	0.058	<0.001	*
Snow	140007	-0.324	0.049	<0.001	*	-0.461	0.043	<0.001	*	0.139	0.038	<0.001	*	0.553	0.052	<0.001	*
Snow	140008	-0.384	0.046	<0.001	*	1.400	0.071	<0.001	*	-0.500	0.036	<0.001	*	-0.456	0.056	<0.001	*
Snow	140010	-0.276	0.037	<0.001	*	-2.132	0.122	<0.001	*	-1.477	0.096	<0.001	*	*NA*	*NA*	*NA*	
Snow	140017	0.016	0.041	0.703		-0.227	0.042	<0.001	*	0.167	0.035	<0.001	*	-0.509	0.042	<0.001	*
Snow	140019	-0.299	0.045	<0.001	*	-0.216	0.043	<0.001	*	-0.169	0.046	<0.001	*	-0.119	0.062	0.055	

Snow	140021	-0.018	0.035	0.613		0.368	0.062	<0.001	*	-0.808	0.063	<0.001	*	*NA*	*NA*	*NA*	
Snow	140027	-0.002	0.041	0.961		-0.307	0.058	<0.001	*	-0.599	0.071	<0.001	*	0.207	0.078	0.008	*
Snow	140030	-0.039	0.064	0.546		-0.820	0.152	<0.001	*	0.153	0.063	0.016	*	*NA*	*NA*	*NA*	
Snow	140037	0.189	0.036	<0.001	*	-0.625	0.053	<0.001	*	0.060	0.054	0.271		-0.174	0.047	<0.001	*
Snow	140038	-0.050	0.035	0.151		0.751	0.070	<0.001	*	-0.200	0.037	<0.001	*	0.334	0.052	<0.001	*
Snow	140039	0.034	0.025	0.173		0.486	0.055	<0.001	*	-0.118	0.028	<0.001	*	0.091	0.034	0.008	*

Appendix E: RSF and LSD maps

E.1 Black bears

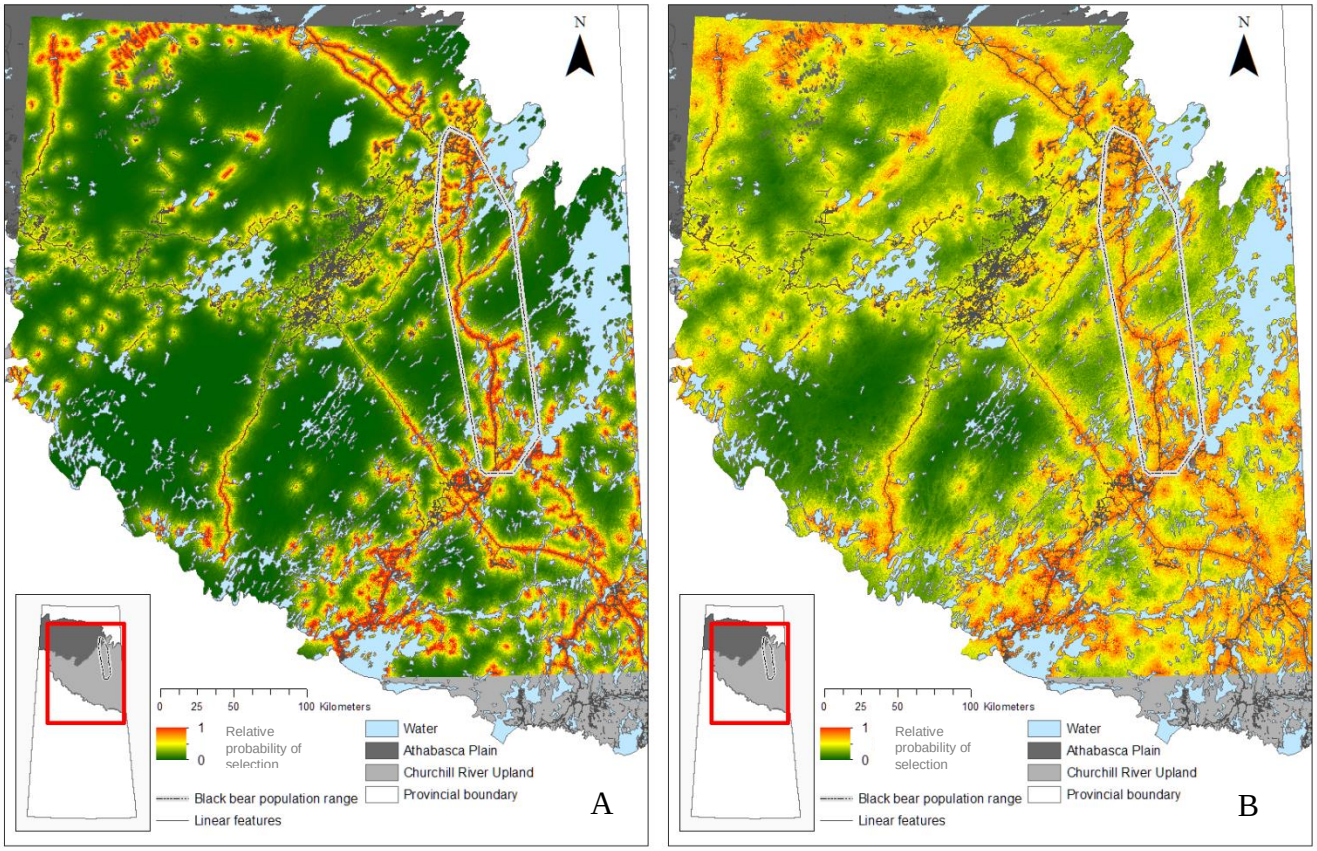

Figure E.1.1. Maps of resource selection functions (RSF) showing relative probability of black bear selection in the Boreal Shield of Saskatchewan at the population (A) and home range (B) scales in the spring season in 2017.

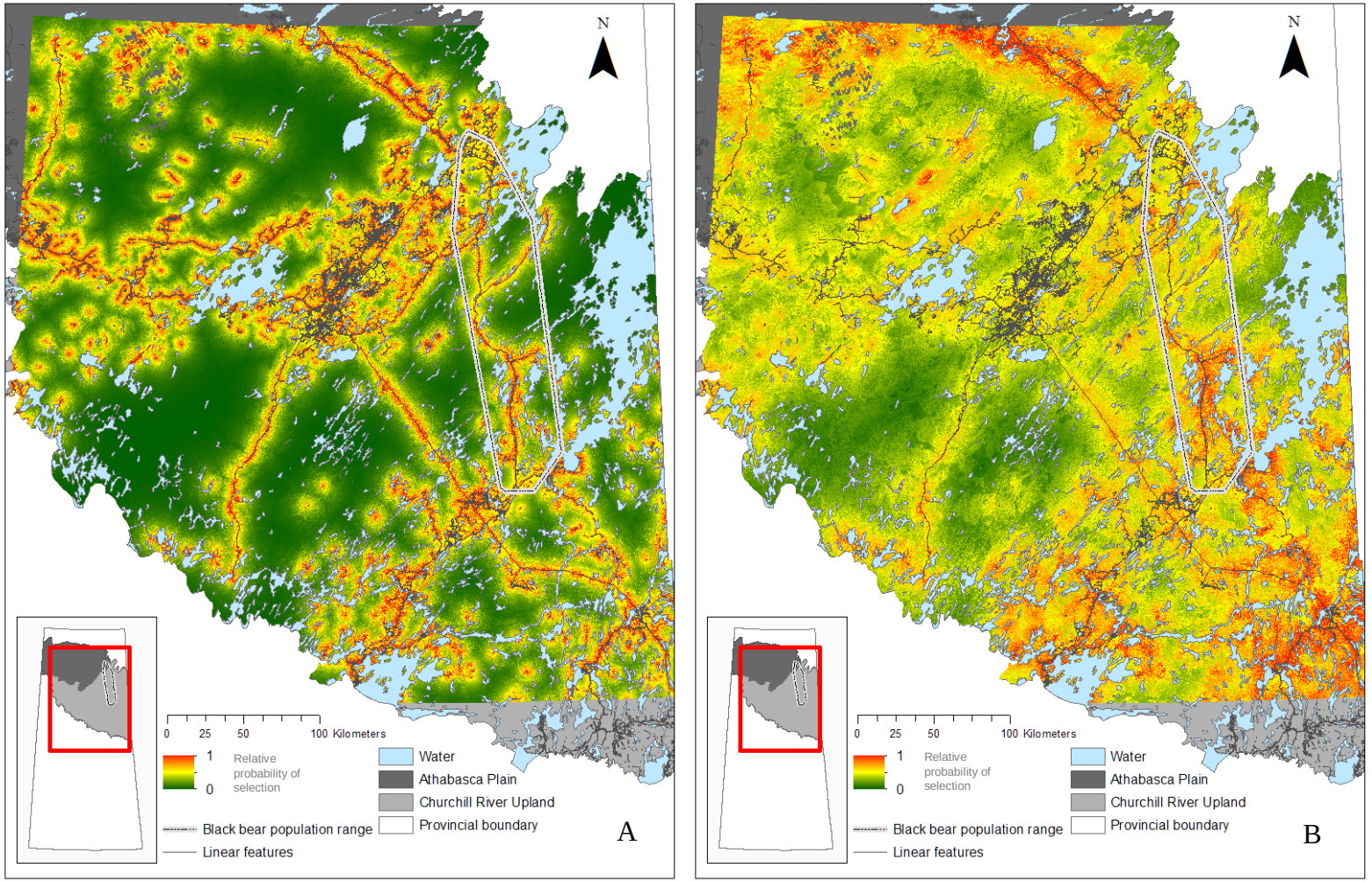

Figure E.1.2. Maps of resource selection functions (RSF) showing relative probability of black bear selection in the Boreal Shield of Saskatchewan at the population (A) and home range (B) scales in the summer season in 2017.

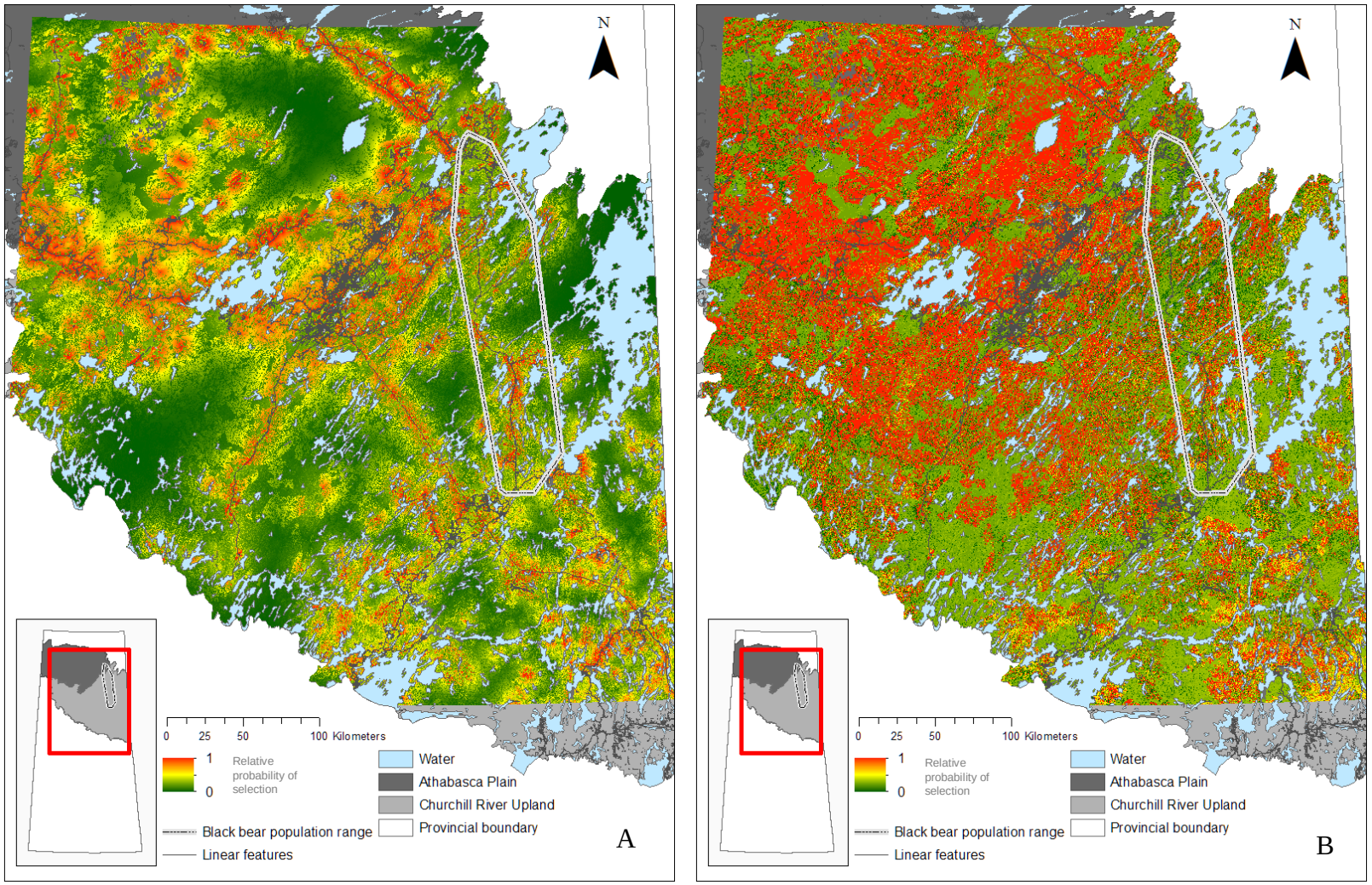

Figure E.1.3. Maps of resource selection functions (RSF) showing relative probability of black bear selection in the Boreal Shield of Saskatchewan at the population (A) and home range (B) scales in the fall season in 2017.

E.2 Gray wolves

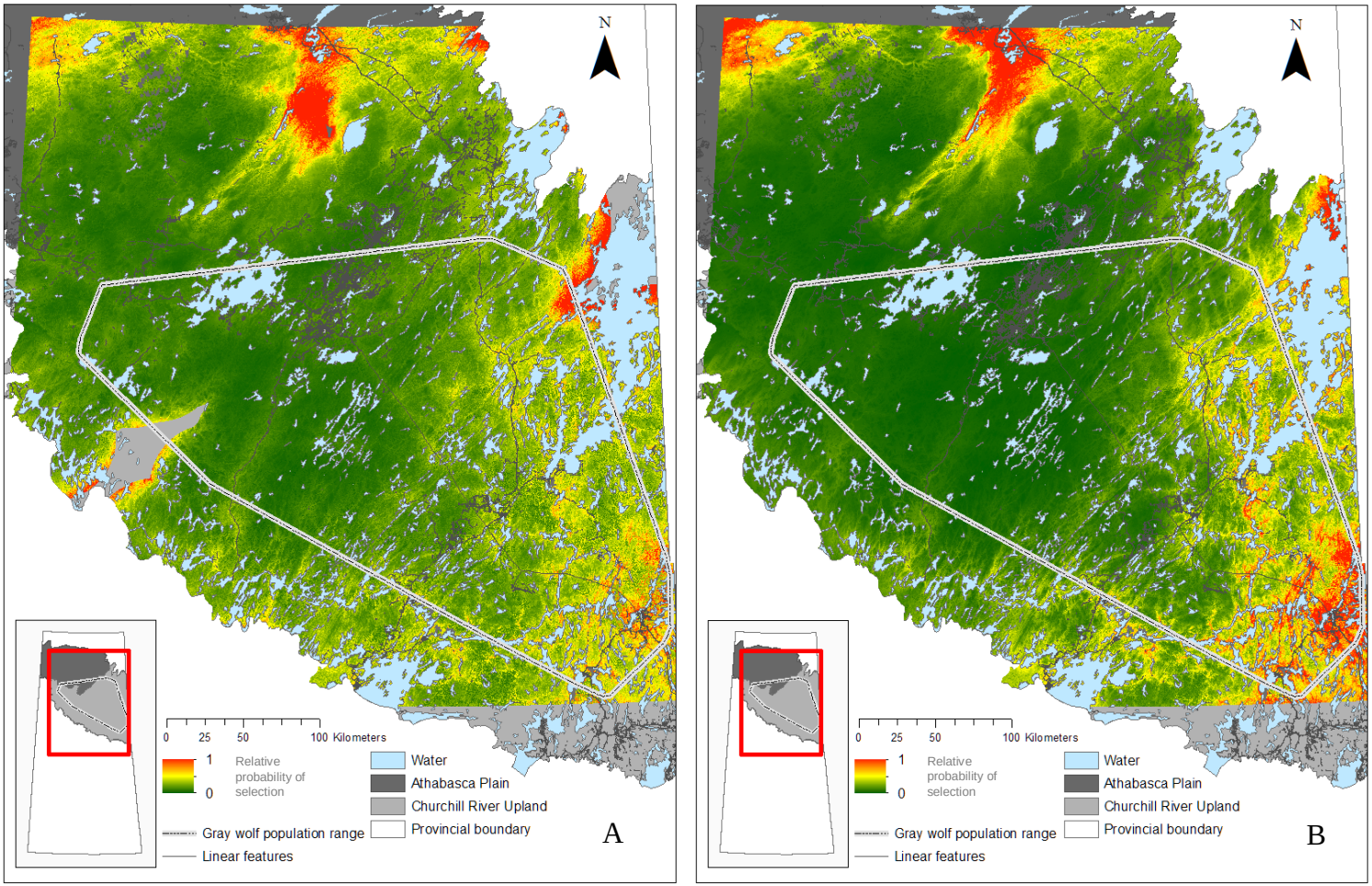

Figure E.2.1. Maps of resource selection functions (RSF) showing relative probability of gray wolf selection in the Boreal Shield of Saskatchewan at the population (A) and home range (B) scales in the snow-free seasons between 2014 and 2015.

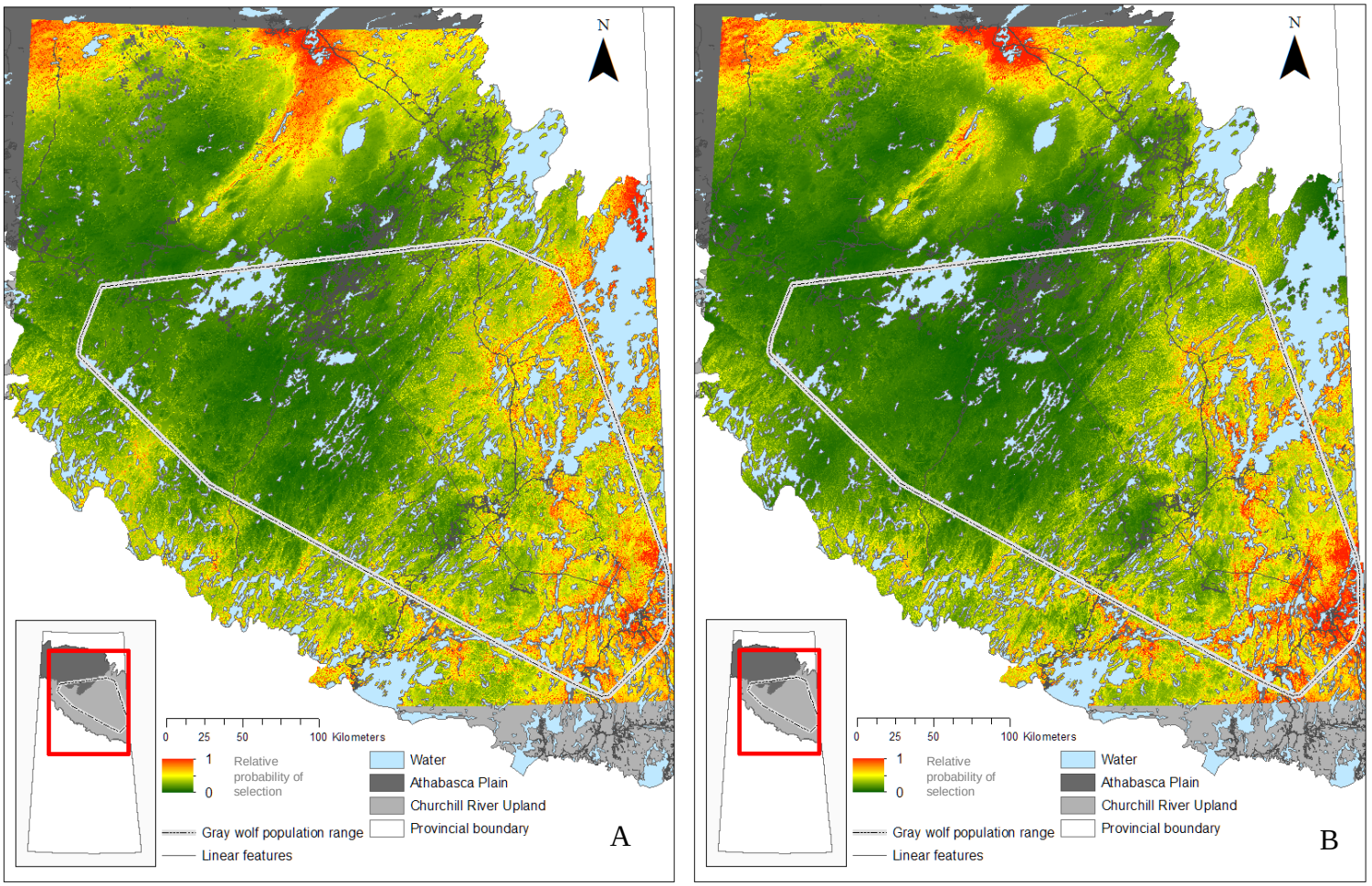

Figure E.2.2. Maps of resource selection functions (RSF) showing relative probability of gray wolf selection in the Boreal Shield of Saskatchewan at the population (A) and home range (B) scales in the snow seasons between 2014 and 2015.

E.3 Comparing species

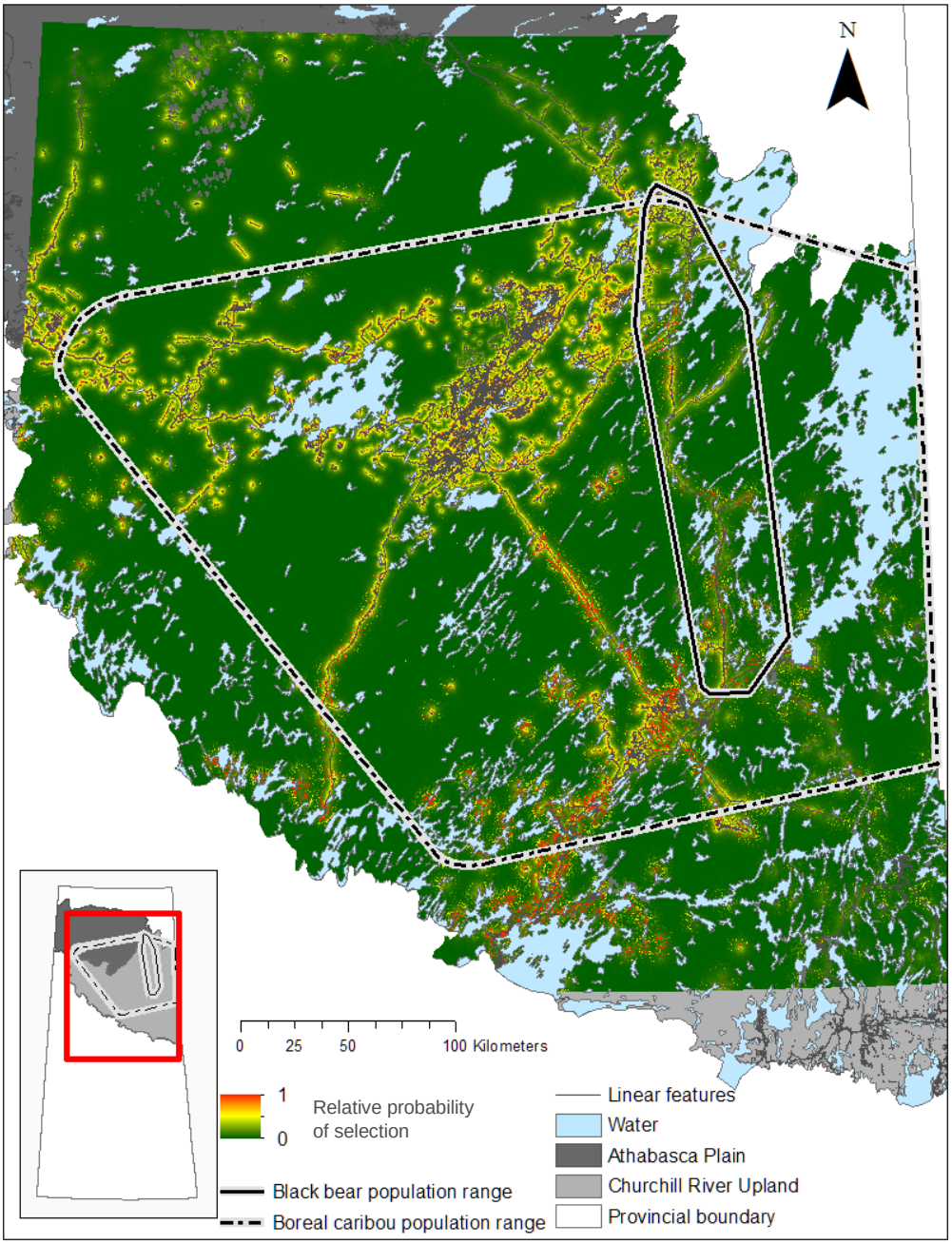

Figure E.3.1. Map of latent selection difference (LSD) showing relative probability of black bear selection relative to boreal caribou in the Boreal Shield of Saskatchewan during the calving and post-calving seasons in 2017.

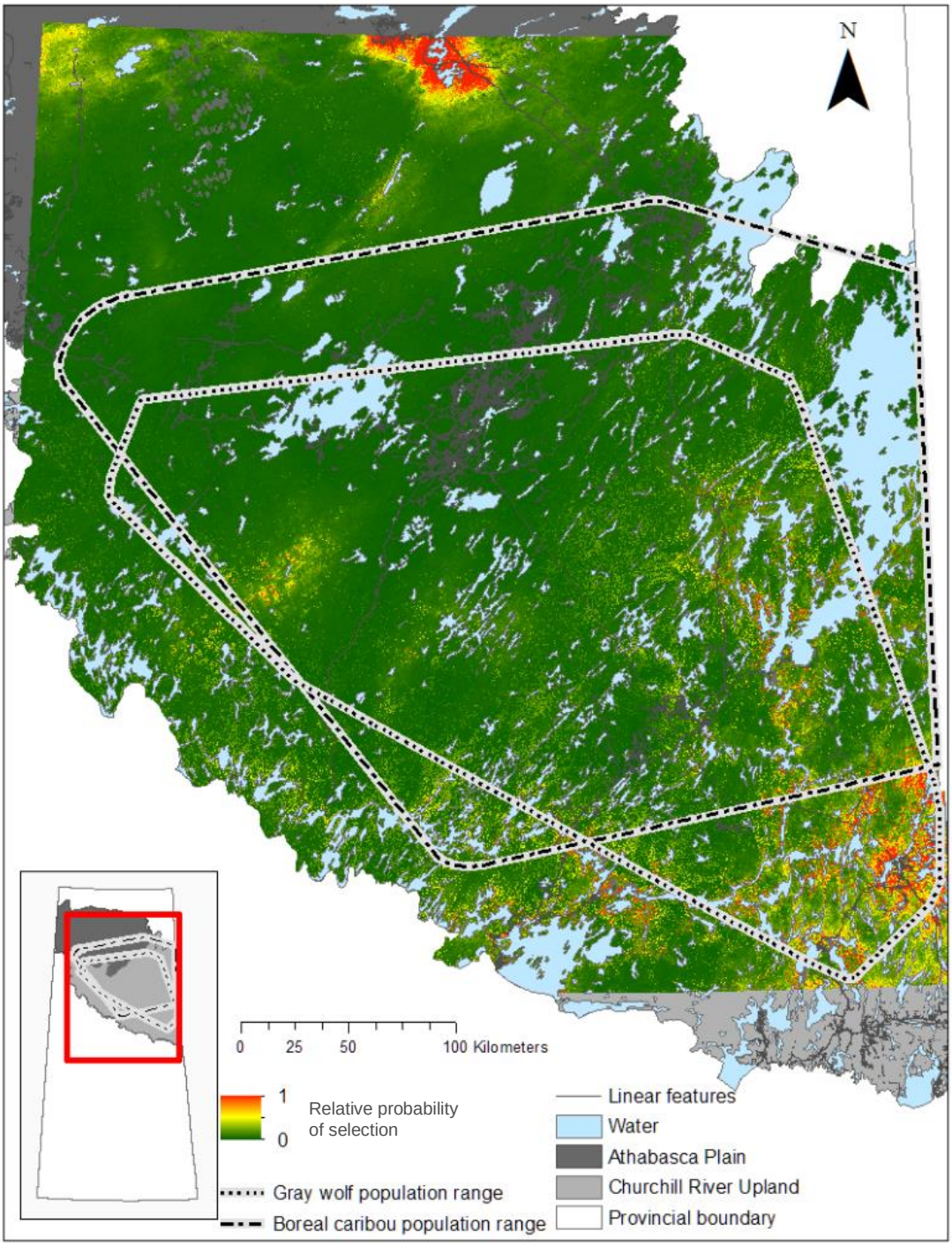

Figure E.3.2. Map of latent selection difference (LSD) showing relative probability of gray wolf selection relative to boreal caribou in the Boreal Shield of Saskatchewan during the calving and post-calving seasons between 2014 and 2015.

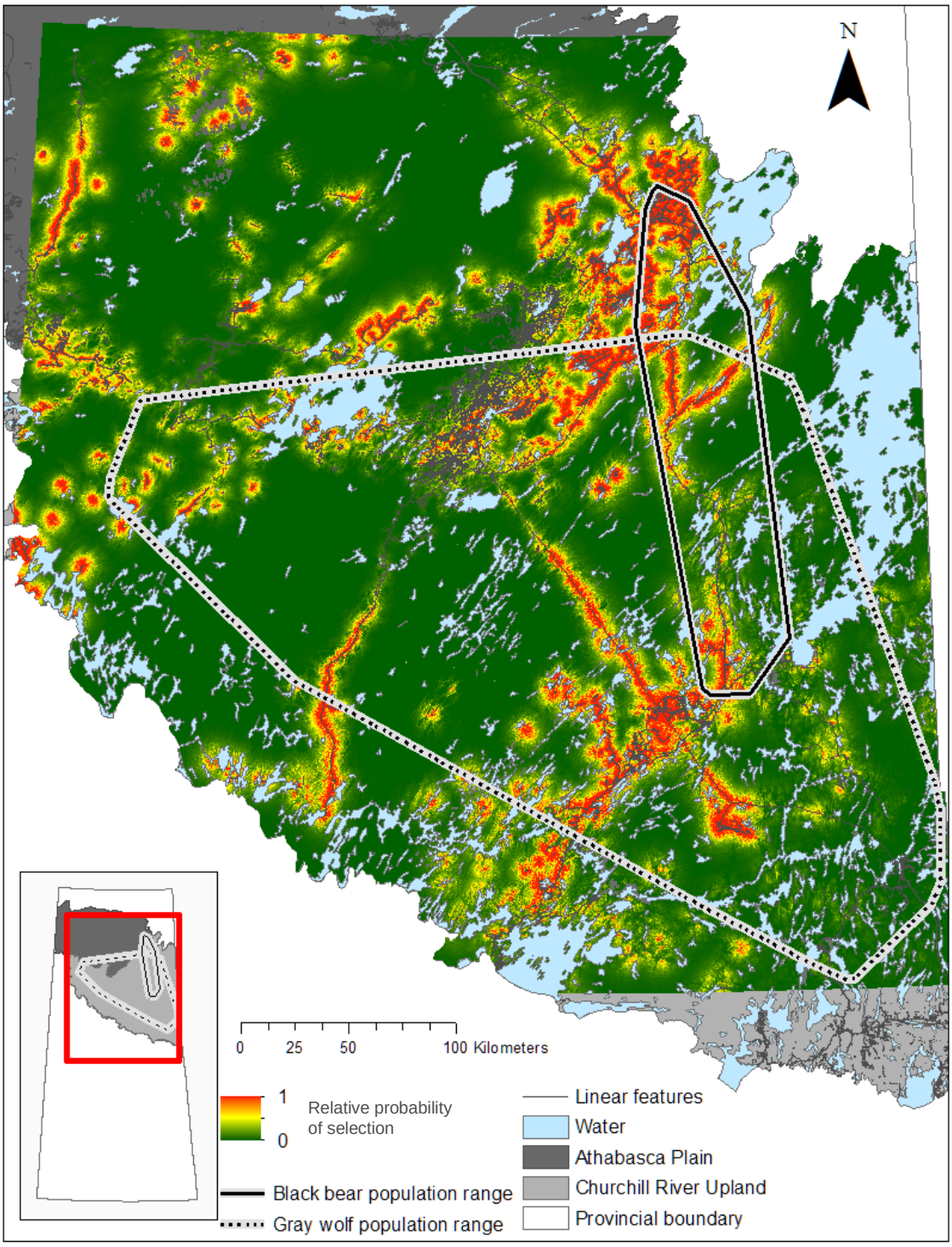

Figure E.3.3. Map of latent selection difference (LSD) showing relative probability of black bear selection relative to gray wolves in the Boreal Shield of Saskatchewan during the calving and post-calving seasons in 2014, 2015, and 2017.